

IMMATURE STAGES OF VENEZUELAN DIOPTINAE (NOTODONTIDAE) IN *JOSIA* AND *THIRMIDA*

JAMES S. MILLER

Department of Entomology, American Museum of Natural History,
Central Park West at 79th Street, New York, New York 10024, USA

AND

L. DANIEL OTERO

Laboratorio de Química Ecológica, Departamento de Química, Facultad de Ciencias,
Universidad de Los Andes, La Hechicera, Mérida 5101, Venezuela

ABSTRACT. Immature stages of five species of Dioptinae (Notodontidae) from Venezuela are described and illustrated. Four are in the genus *Josia* Hübner and one is in *Thirmida* Walker. All feed as larvae on *Passiflora* (Passifloraceae). This is the first life history reported for a member of *Thirmida*. Immature stages are described for each species, and distributional and hostplant data are provided. The tribe Josiini, formerly a subfamily (Josiinae), is delineated. It comprises 103 species in eleven dioptine genera. *Josia turgida* and *Thirmida discinota*, treated by previous authors as subspecies, are revised to species status.

Additional key words: Josiini, *Passiflora*, montane forest, larval morphology.

The Neotropical moth subfamily Dioptinae is unique among Notodontidae in containing many diurnal forms with aposematic color patterns (Hering 1925, Köhler 1930, Miller 1992a). The group includes over 400 described species (Byrk 1930), most of which are poorly represented in museums worldwide. The most commonly collected dioptines are those in *Josia*, a genus distributed from southern Mexico south to northern Argentina. *Josia* adults are strikingly colored, usually with orange or yellow markings against a dark ground color, and they tend to fly in a slow, fluttering manner. The caterpillars, which feed on plants in the genus *Passiflora* (Passifloraceae), commonly called "passion flowers," are conspicuously patterned with various hues of reddish maroon, yellow, and white.

Among Lepidoptera only two large species radiations are associated with *Passiflora*—*Josia* and its relatives, and members of the butterfly subfamily Heliconiinae (Nymphalidae). *Heliconius*, containing approximately 70 Neotropical species (Brown 1981, DeVries 1987), has been the subject of intense ecological and evolutionary research, and an immense amount of biological data has accumulated. For example, there are over 350 published host records for the genus (Benson 1978). In contrast, the amount of biological information available for *Josia* is minute; hosts are recorded for only five species, all from Brazil (Spitz 1931, d'Almeida 1932, Bienzanko 1962a, 1962b, Silva et al. 1968). In this paper we describe the immature stages of five *Passiflora*-feeding Dioptinae from Venezuela.

TABLE 1. Genera belonging in the tribe Josiini (Notodontidae: Dioptinae) based on presence of a kettle-drum metathoracic tympanum in the adult (see text). Generic names follow Watson et al. (1980). Numbers of species for each genus are from Bryk (1930).

Genus	Number of included spp.
<i>Leptactea</i> Prout	1
<i>Mitradaemon</i> Butler	5
<i>Josia</i> Hübner	68
<i>Scea</i> Walker	12
<i>Thirmida</i> Walker	6
<i>Cyanotricha</i> Prout	2
<i>Phavaraea</i> Walker	2
<i>Scedros</i> Walker	1
<i>Getta</i> Walker	3
<i>Anticoreura</i> Prout	1
<i>Polyptychia</i> Felder	2
Total number of species	103

Previous systematic studies have shown that *Josia* belongs in a large, well-defined clade that includes other dioptine genera. Below, we review the evidence supporting that hypothesis.

The Tribe Josiini

Most notodontid adults have a relatively simple metathoracic tympanum (Surlykke 1984, Scoble 1992) characterized by a shallow dorsal invagination of the epimeron, with the tympanal membrane above, facing postero-ventrally. Richards (1932), in his classic study of noctuid tympanal morphology, described a unique type, which he termed the "kettle-drum" tympanum, found in the dioptine genera *Cyanotricha* and *Josia*. In these genera, the epimeron is greatly invaginated to form a large, enclosed chamber. The tympanal membrane, oriented horizontally, forms the ceiling of the chamber (the "head" of the kettle-drum). The chamber opens to the outside by means of a small lateral hole. The kettle-drum tympanum is figured in Börner (1939: fig. 41), Sick (1940: figs. 1-4), Kiriakoff (1950: figs. 9, 10), and Miller (1991: fig. 240).

After studying tympana throughout the Dioptinae, Sick (1940) created "Group V" for those genera with a kettle-drum tympanum. Group V contained eight genera: *Mitradaemon* Walker, *Josia* Hübner, *Scea* Walker, *Thirmida* Walker, *Cyanotricha* Prout, *Phavaraea* Walker, *Getta* Walker, and *Polyptychia* Felder. Kiriakoff (1950) also noted the highly derived tympanum of *Josia*. He divided the "Dioptidae" into two subfamilies: the Dioptinae with a simple tympanum and the Josiinae with a kettle-drum tympanum. Although Kiriakoff examined fewer



FIG. 1. Map of Venezuela; state boundaries shown with dashed lines (scale bar = 100 km).

taxa than Sick, his list of genera for the Josiinae corresponds closely with Group V. Recent findings have shown that, rather than being a separate family as previous authors had supposed, the Dioptinae is a highly derived subfamily within the Notodontidae (Minet 1983, Weller 1989, Miller 1991, 1992b). Kiriakoff's divisions thus can be recognized as tribes, the Dioptini and Josiini (*new status*).

We performed an exhaustive survey of tympanal structure in the Dioptinae. In addition to the eight genera in Sick's (1940) Group V, we discovered three monobasic genera with the kettle-drum tympanum: *Leptactea* Prout, *Scedros* Walker, and *Anticoreura* Prout. According to our definition, the tribe Josiini includes 103 described species in 11 genera (Table 1).

Previous Works on the Josiini

Although early authors did not formally recognize the Josiini, they nevertheless provided relevant taxonomic treatments of the group. The

two most important are Prout's (1918) preliminary revision of dioptine genera and Hering's (1925) contribution to Seitz, where species diagnoses are provided and adults of many taxa are figured. Two keys to *Josia* adults are available, one in Walker (1854: 289-290), and a more complete one in Forbes (1931). Forbes (1939) also gave keys and diagnoses for five josiines from Barro Colorado Island, Panama.

Morphological and biological data are scant. Markin et al. (1989) described the biology and life stages of *Cyanotricha necyria* Felder, a josiine species from the western Andes. Miller (1988) described the genitalia and copulatory mechanism of *C. necyria*, and also has discussed various features of josiine larval and adult morphology within the context of a reclassification of the Notodontidae (Miller 1991). Papers by other authors give only anecdotal information on immatures. Because of the paucity of published work on the Josiini, we have chosen to present considerable detail in this paper.

METHODS

During the course of our research we visited sites in mountain systems of the Cordillera de la Costa in the state of Aragua of northern Venezuela, and in the Cordillera de Mérida in western Venezuela, specifically in the states of Mérida and Barinas (Fig. 1). Our collecting covered a range of elevations (540 to 2420 m), life zones, and vegetation types. We use Holdridge's life zone system, relying on the work of Ewel et al. (1976) to identify life zones for each of our collecting sites. Life zone types are indicated by an abbreviation in parentheses after the locality. The altitudes provided are plus or minus 50 m.

Most of our collecting sites showed varying degrees of habitat disturbance, usually due to agriculture. Large tracts of land in the Cordillera de Mérida and Cordillera de la Costa have a long history of agricultural use, and the vegetation currently present, even in some forested sites, may be secondary. Primary vegetation is often reduced to relictual patches or is limited to steep mountain slopes. Four of our collecting sites are within the limits of national parks, Parque Nacional Henri Pittier in the state of Aragua, and Sierra Nevada in Mérida. In these officially protected areas, the vegetation is likely to be primary.

Passiflora leaves with eggs or larvae of Josiini were picked in the field and transported to the laboratory inside moistened plastic containers. In the lab, leaves were transferred into small glass flasks containing water, submersing the petiole, and plugging the neck of the flask around the petiole with wet paper. Each flask was placed in a plastic dish and covered with an inverted 1 liter transparent plastic container. Leaves usually remained fresh in the rearing containers for

several days. Fresh food was provided when leaves were consumed or showed signs of deterioration.

For two of the species, *Josia radians* and *J. aurifusa*, adult females were collected in the field, placed in plastic bags with host foliage, and brought to the lab. Females laid eggs on the enclosed leaves over a period of two to three days.

Larvae were fed leaves of the *Passiflora* upon which they were discovered in the field, or on an alternative species when the original host was not easily available. Certain of the josiines lay eggs in batches. For these, egg masses were divided and reared in more than one container. Frass accumulations were discarded regularly. Instar durations were not monitored precisely; we therefore give only the approximate development time from field-collected egg to adult emergence. At least for the first, second, and third instars, each stadium lasts approximately five or six days.

We preserved specimens of eggs, first and last instar larvae, and adults. Larvae were preserved by dropping them into hot water (just below boiling temperature) for several seconds, and then transferring them to vials of 70% ethanol. Shed head capsules were saved in alcohol along with the associated specimens. Pupal exuviae were mounted on the same pin as the adult voucher. Voucher material is deposited in the collections of the Museo del Instituto de Zoología Agrícola, Maracay (MIZA) and the American Museum of Natural History, New York (AMNH).

Identifications of adult moths were confirmed by comparison with type specimens. Comparisons between genitalic dissections of vouchers and types were required for *Josia radians*, *J. aurifusa*, and *J. turgida*. These three belong to difficult species complexes, the resolution of which will require study of large series from a wide range of localities. This was beyond the scope of the present work.

The Passifloraceae contains twenty genera and approximately 600 species (Heywood 1979). Over 400 species are placed in the genus *Passiflora*, with all but 20 occurring in the Neotropics (Holm-Nielsen et al. 1988, Gentry 1993). Stephan S. Tillet (Herbario Ovalles, Facultad de Farmacia, Universidad Central de Venezuela, Caracas) verified host-plant identifications. We assign *Passiflora* species to subgenera following Killip (1938), who recognized 22 subgenera for the American flora. However, the classification of *Passiflora* currently is undergoing revision (J. MacDougal and C. Feuillet, pers. comm.), so these assignments are provisional. Plant distributions are based on Killip (1938) and Holm-Nielsen et al. (1988).

Nomenclature for larval morphology follows Stehr (1987) and Pe-

terson (1962). We employ the system for larval chaetotaxy developed by Hinton (1946), but have incorporated minor modifications suggested in Miller (1991) and Rawlins (1992). For first instars we use the setal nomenclature of Kitching (1984) on Danaini (Nymphalidae) and Fleming (1960) on Heliconiinae. Pupal terminology follows Mosher (1916). Larval measurements were made using a Microcode II (Boeckeler Instruments) digital micrometer attached to a Zeiss SV8 stereomicroscope. Electron micrographs were taken with a Zeiss DSM 950 Digital Scanning Microscope.

Abbreviations. A = abdominal segment; CuA = cubital wing vein; D = dorsal seta; DC = discal cell; FW = forewing; HW = hindwing; JSM = James S. Miller; L = lateral seta; LDO = L. Daniel Otero; LM-mf = lower montane moist forest; LM-wf = lower montane wet forest; M = medial wing vein; P = posterior seta; PM-df = premontane dry forest; PM-mf = premontane moist forest; PM-wf = premontane wet forest; R = radial wing vein; SD = subdorsal seta; SV = subventral seta; T1 = prothoracic segment; T2 = mesothoracic segment; T3 = metathoracic segment; T-mf = tropical moist forest; TS = tarsal seta; V = ventral seta. (Additional abbreviations are given in the figure legends.)

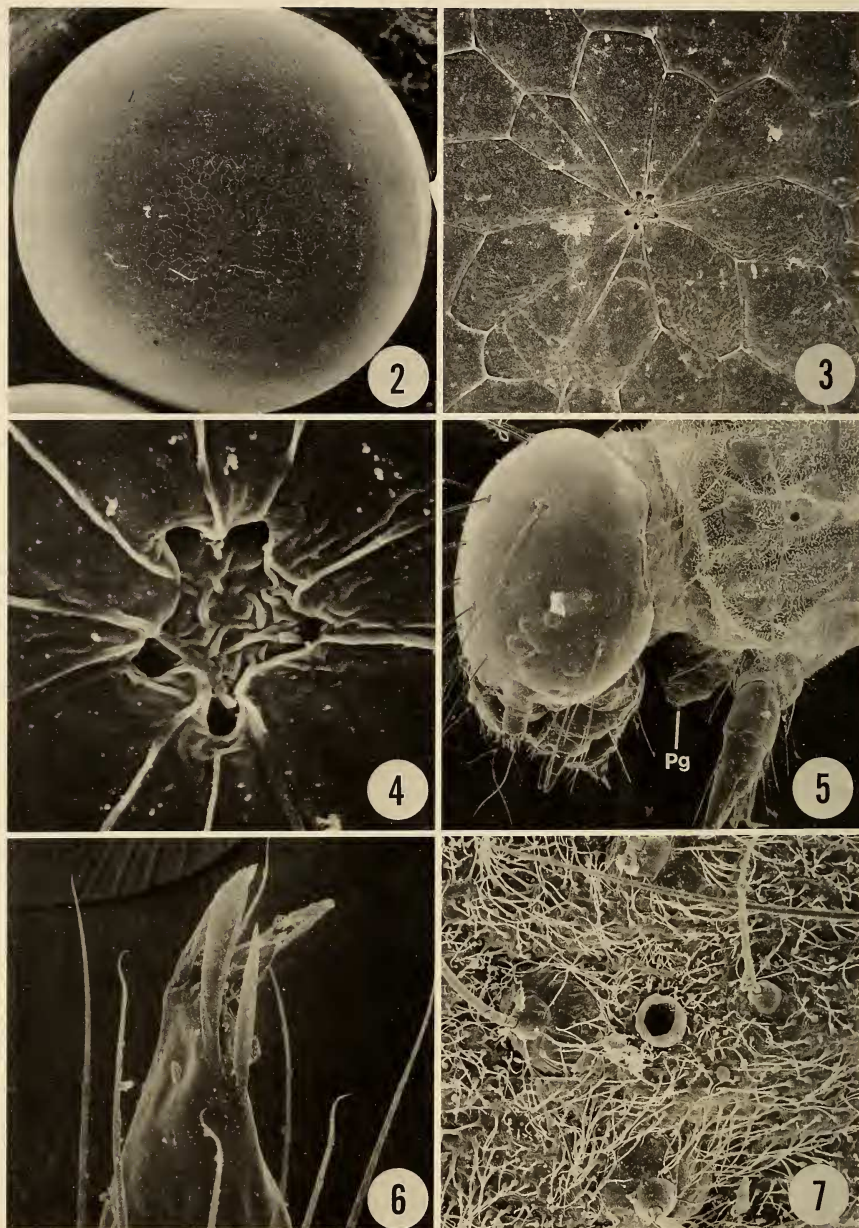
Acronyms for Museums. AMNH = American Museum of Natural History, New York, NY; BMNH = The Natural History Museum, London, Great Britain; CMNH = Carnegie Museum of Natural History, Pittsburgh, PA; CUIC = Cornell University Insect Collections, Ithaca, NY; LACM = Los Angeles County Museum of Natural History, CA; MIZA = Museo del Instituto de Zoología Agrícola, Maracay, Venezuela; MNHN = Muséum National d'Histoire Naturelle, Paris, France; NMNH = National Museum of Natural History, Washington, DC; ZMH = Zoologisches Museum, Humboldt-Universität, Berlin, Germany.

GENERAL ACCOUNT

Many of the traits we observed are found throughout our study taxa. General morphological features, as well as those that provide potentially useful taxonomic differences, are summarized below.

Egg. The pearly white eggs are almost perfectly spherical (Figs. 2, 15), without surface sculpturing except for a fine reticulate pattern in the area surrounding the micropyle (Figs. 3, 4). Among the five study species, egg size ranges from 0.70 to 1.10 mm in diameter. They are laid either individually, or in small clusters of up to 25 eggs (Fig. 15).

First Instar Larva. All first instars in this study exhibit the same simple primary setal pattern (Figs. 47, 56, 71, 78); setae L2 and L3 absent on segments T2 and T3, L3 absent on A1–A7. This configuration also occurs in first instars of Nymphalidae (Kitching 1984), Heliconiinae (Fleming 1960), and Noctuidae (Merzheevskaya 1988), and is probably



FIGS. 2-7. Scanning electron micrographs of *Thirmida discinota* immature stages. 2, Egg, dorsal view ($\times 79$); 3, Micropyle and surrounding area ($\times 1263$); 4, Micropyle ($\times 6960$); 5, Head and T1 of first instar, lateral view ($\times 97$); 6, Tarsus of first instar T3 leg, mesal view ($\times 596$); 7, A8 spiracle and setal bases, first instar ($\times 344$). [Pg = prothoracic gland.]

distributed throughout the Lepidoptera. Features restricted to first instar larvae include: antenna short (Figs. 5, 48, 61, 79); spinneret long and apically acute (Figs. 5, 48, 61, 79); mandible serrate (Godfrey et al. 1989); tarsal setae elongate (Figs. 6, 49); each primary seta located on a prominent, sclerotized pinaculum (Figs. 5, 7, 47, 56, 71, 78); spiracles extremely small, round (Figs. 5, 7); color pattern simple, either entirely white or with alternating reddish bands (compare Figs. 47 and 56).

Fourth (Final) Instar Larva. Subprimary setae are defined as those that appear after the first larval molt (Hinton 1946, Kitching 1984). In the josiines we studied, second, third, and fourth instars have the same setal pattern. However, patterns can vary between species, suggesting that subprimary setae may be useful in josiine systematics. For example, fourth instars of *Josia gopala* possess an L seta on segments A2–A6 not found in other species (compare Figs. 52 and 67). In *Thirmida discinota*, L3 on A3–A6 is multiple, and there are novel setae on the anal plate (Figs. 43, 44). Characters such as these may provide useful synapomorphies for defining subclades within the Josiini. Color pattern differences provide important characters for separating species.

A diagnosis of last instar larval morphology for Josiini is as follows: Head either entirely black (Fig. 45), or white with dark dorso-ventral stripes (Figs. 54, 69, 76, 85); mandibular margin smooth (Godfrey et al. 1989); antenna with segment 2 longer than segment 1, segment 3 short (Figs. 10, 51, 80, 81); spinneret short and wide (Figs. 11, 50, 62). Primary setal pattern generally as in other Notodontidae; secondary setae occasionally present on head and body (in *Cyanotricha necyria*; Miller 1991); tarsal setae TS2 and TS4 lanceolate with apices acute, TS3 broad, leaf-shaped (Figs. 12, 13, 57, 63, 82); prothoracic gland present (Figs. 8, 9, 43, 52, 67, 74, 83); thorax and abdomen lacking projections, but with a slight hump on A8 (Figs. 44, 53, 68, 75, 84); cuticle glossy in appearance, covered with microprojections (=“shagreened;” e.g., Figs. 5, 7, 20–23); body variously patterned with reddish maroon, yellow and white (Figs. 14–19); A8 spiracle either subcircular or an elongate oval (Figs. 21–23); terminal segments often conspicuous, white (Figs. 16–19); prolegs on A10 reduced but functional (Figs. 44, 53, 68, 75, 84); segments A7–A10 frequently held aloft (Figs. 16, 18, 19); like other Dioptinae (but unlike other Notodontidae), a single MD seta on A1 rather than two (Miller 1991).

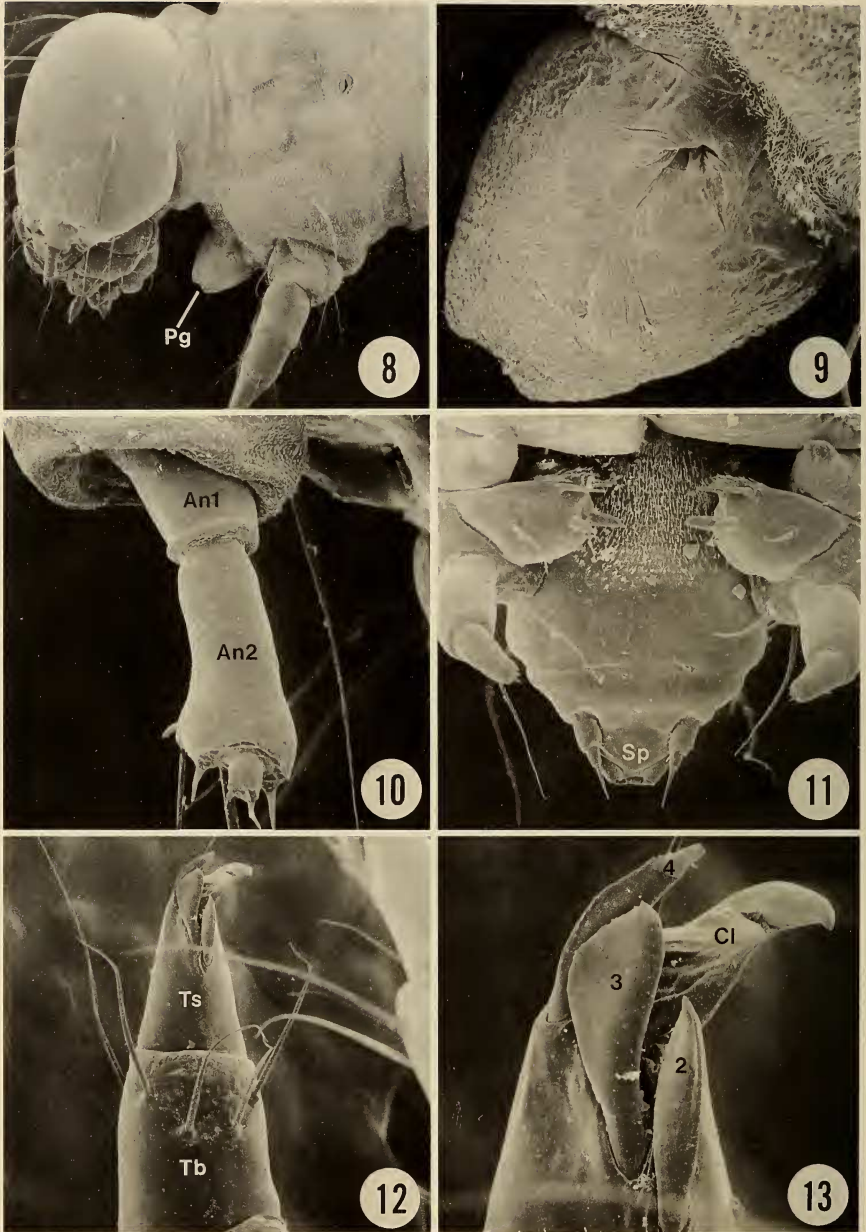
Pupa. Most features of josiine pupal morphology do not show significant variation (see Miller 1992b: figs. 31, 32). However, the cremaster varies in shape, and in the number and size of the cremaster setae (Figs. 24, 25, 58–60, 64–66).

Adult. Many external adult traits show variation, and these can be used in identification. Examples include the shape of the labial palpus and length of the pectinations on the male antenna. The forewing can exhibit a longitudinal stripe (Figs. 28–36), a transverse one (Hering 1925), or variations on the latter (Figs. 26, 27). The species of Josiini also differ greatly in size; FW lengths range from 11 mm (*Josia ena* Boisduval) to 28 mm (*Phavaraea rejecta* Hübner).

SPECIES ACCOUNTS

Thirmida discinota Warren, 1900, revised status

Distribution. This species is known almost exclusively from localities close to the city of Mérida. However, a single specimen (MIZA) from the State of Lara has the following data: Parque Nacional Yacambú, El Blanquito, 1350 m; 1–3/VIII/1976; C. J. Rosales, L. J. Joly. This is the lowest elevation from which *T. discinota* is known; all the other specimens were collected at or above 2000 m. Data for the female holotype (BMNH) is given as Pedregosa, Mérida, 3000 m, October 1897 (Briceño) (Warren 1900:129), a locality southwest of the city of Mérida. *Thirmida discinota* is rare in collections. Previously it was represented



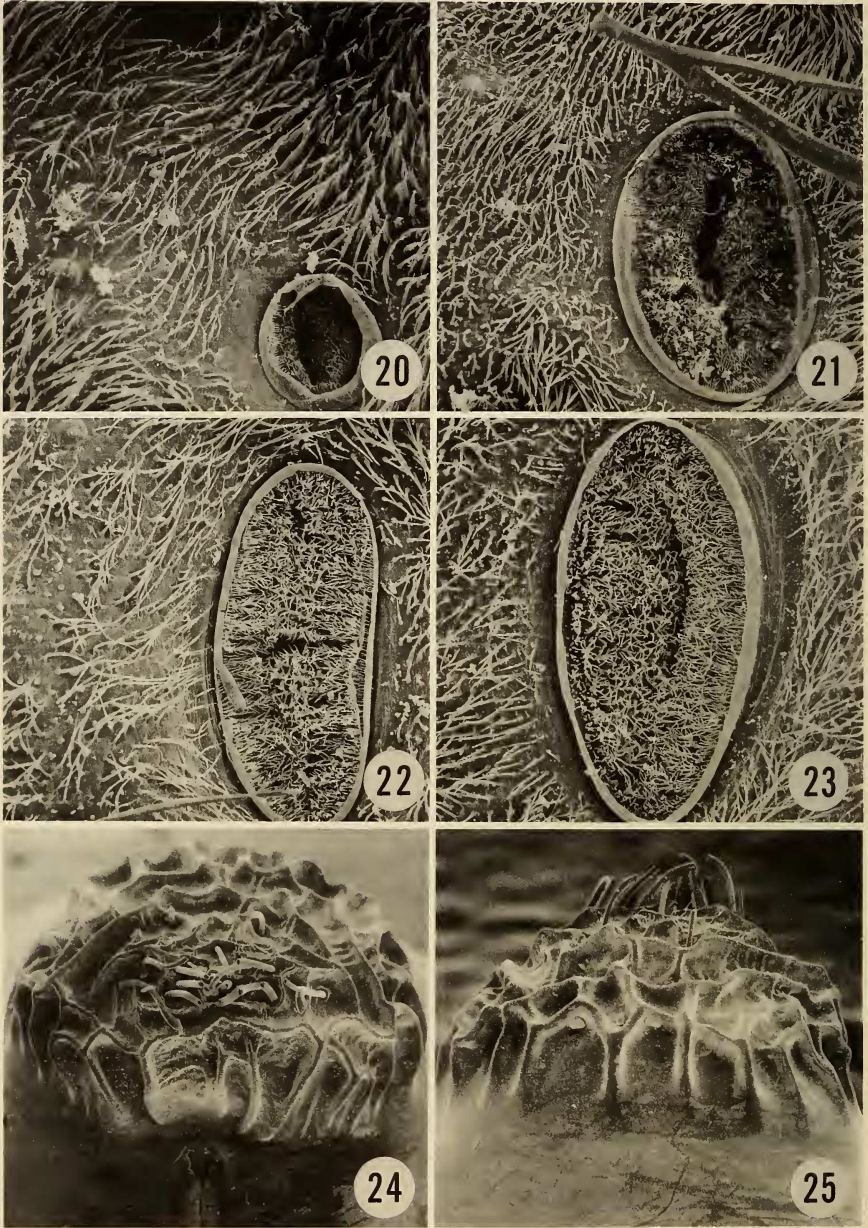
FIGS. 8-13. Scanning electron micrographs of fourth instar *Thirmida discinota* larva. 8, Head and T1 ($\times 22$); 9, Prothoracic gland, lateral view ($\times 133$); 10, Antenna, frontal view ($\times 180$); 11, Maxillary and hypopharyngeal complexes, frontal view ($\times 133$); 12, Tibia and tarsus of right T2 leg, mesal view ($\times 82$); 13, Tarsus of right T2 leg, mesal view ($\times 290$). [An = antennal segment; Cl = tarsal claw; Pg = prothoracic gland; Sp = spinneret; 2, 3, 4 = tarsal setae 2, 3, and 4.]



FIGS. 14-19. Immature stages of Josiini. 14, Fourth instar larva of *Thirmida discinota* on *Passiflora bauhinifolia*; 15, Eggs of *Thirmida discinota* laid on the underside of *P. bauhinifolia* leaves; 16, Fourth instar of *Josia radians* on *Passiflora capsularis*; 17, Fourth instar larva of *Josia gopala* on *Passiflora cuneata*; 18, Fourth instar larva of *Josia aurifusa* on *P. capsularis*; 19, Fourth instar larva of *Josia turgida* on *P. capsularis*. Photographs by L. Daniel Otero.

in major museums by a total of 13 specimens (BMNH, MIZA, NMNH, and ZMH), most of which were collected near the turn of the century. We have found it to be locally abundant.

Collecting Localities. Recorded from Quebrada La Caña on the road from El Valle to La Culata, northwest of Mérida, at 2420 m (31 October



FIGS. 20-25. Scanning electron micrographs of Josiini immature stages. 20, A4 spiracle, fourth instar *Thirmida discinota* larva (note seta MSD2 at left) ($\times 211$); 21, A8 spiracle, fourth instar *T. discinota* larva ($\times 151$); 22, A8 spiracle, fourth instar *Josia aurifusa* larva ($\times 248$); 23, A8 spiracle, fourth instar *Josia radians* larva ($\times 243$); 24, Cremaster of *T. discinota* pupa, postero-ventral view ($\times 58$); 25, Cremaster of *T. discinota*, dorsal view ($\times 59$).

1992, 17 January 1993, and 6 April 1993). The life zone for this locality is regarded as lower montane moist forest (LM-mf) according to Ewel et al. (1976). However, only relictual patches of the original forest type remain, and the habitat where we found *T. discinota* is characterized by secondary vegetation that includes shrubs and some small trees (Fig. 42).

Foodplant. Eggs of *T. discinota* were collected on vines of *Passiflora bahuinifolia* Kunth (subgenus *Plectostemma*), growing near a stream. There is some confusion regarding the distribution and taxonomic status of this species; Holm-Nielsen et al. (1988) regard it as a synonym of *P. alnifolia* Kunth, and according to Killip (1938) the plant occurs only in southwestern Colombia, Ecuador, and northern Peru.

Egg. Relatively large (1.1 mm; $n = 5$); deposited in clusters of 4 to 25 eggs (Fig. 15). Eggs tend to be laid on older leaves than in the other Josiini that we observed. Markin et al. (1989) noted a similar preference for mature foliage by ovipositing females of *Cyanotricha necyria* Felder (Josiini). Based on field collections, duration of the egg stage is at least 10 days. Development time from field-collected egg to adult = 60–65 days.

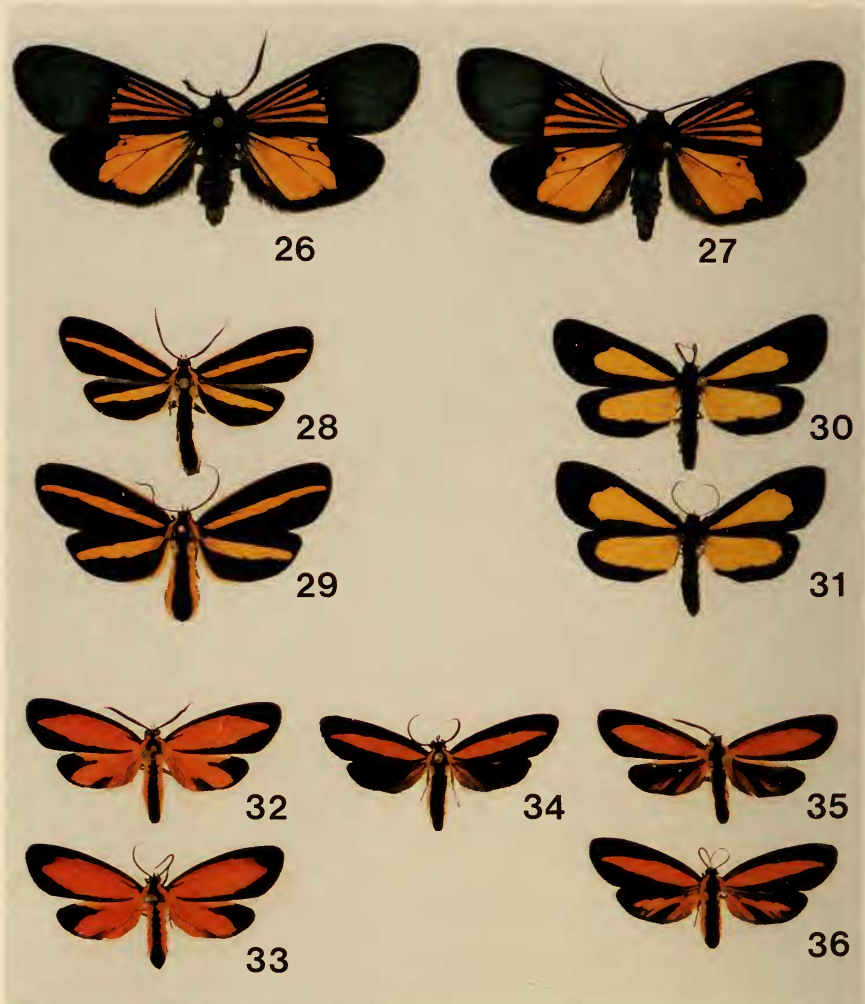
First Instar. Head entirely black except for white clypeus; thorax and abdomen unpigmented. Primary setae (Fig. 47) as in general account (above), similar to *Josta*. Body length = 5.24–5.58 mm; head width = 0.77–0.78 mm ($n = 5$).

Second and Third Instars. Similar in setal and pigment patterns to final instar larvae. Head widths: 2nd instar = 1.14–1.22 mm; 3rd instar = 1.80–1.88 mm ($n = 5$).

Final (Fourth) Instar. Head entirely shiny black except for white clypeus and thin white lines along ecdysial suture and ecdysial lines (Fig. 45); labrum with a whitish central area; antenna with segment 2 expanded distally, approximately twice the length of segment 1. Prothoracic shield (Fig. 46) broad, heavily sclerotized, with a partial medial seam, anterolateral angles not produced; ground color of thorax and abdomen reddish purple (Fig. 14); a lemon yellow longitudinal stripe along dorsal midline bordered on each side by a thin, irregular whitish subdorsal stripe; lateral pattern complex (Figs. 43, 44), composed of a wide yellow longitudinal stripe with reddish purple blotches and an irregular reddish purple stripe within it; venter entirely lemon yellow; segment A9 not conspicuous, mostly maroon above. Tarsal setae with TS2 and TS4 lanceolate, TS3 broad and leaf-shaped, apex emarginate (Fig. 13). Setal pattern (Figs. 43, 44) on thorax and abdomen similar to other Josiini, but with the following exceptions: seta SV2 on segment A2 located between L3 and SV3, on a horizontal line with them; one or two additional setae present on proleg-bearing segments (A3–A6) in the L3 position; anal plate with 2–3 additional setae on each side; lateral plate of A10 proleg base with more than 12 setae; all primary setae wide, white and “fleshy” in appearance; each thoracic and abdominal seta on a small, heavily sclerotized pinaculum. Body length = 38.0–39.0 mm; head width = 2.60–2.83 mm ($n = 5$).

Pupa. Cremaster (Figs. 24, 25) short and broad, heavily rugose dorsally with broad, longitudinal flutes ventrally; approximately 20 short, hook-shaped setae. Duration: approximately 20 days.

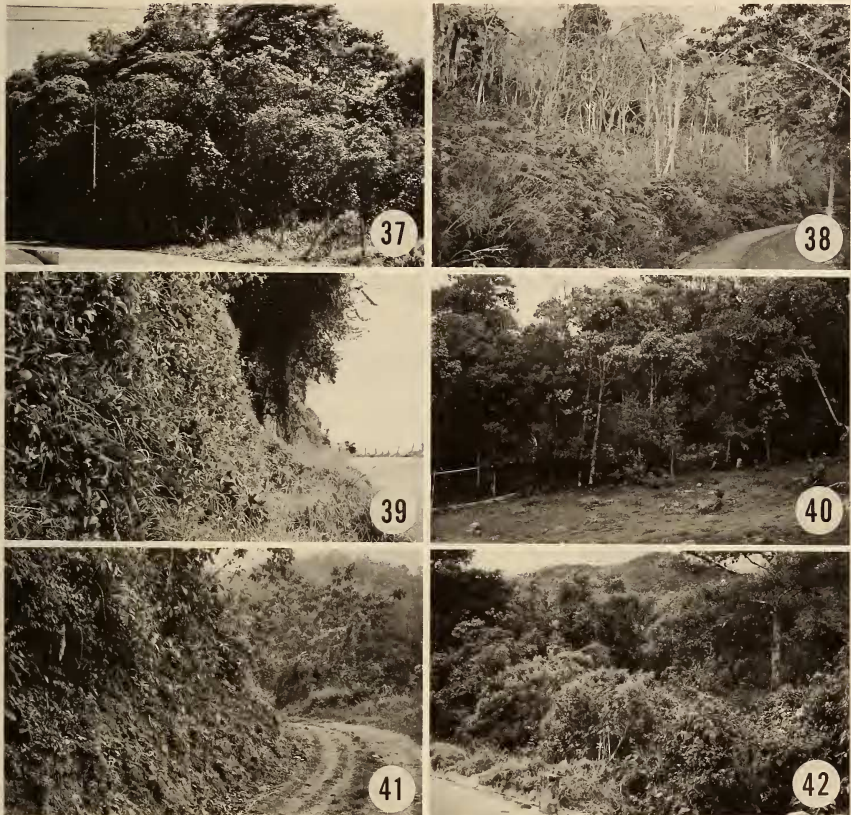
Adult. FW length = 23–25 mm. Head, thorax and abdomen gray-brown, abdomen with scattered iridescent bluish scales; pectinations of male antenna long; eye relatively small; front and labial palpus rough-scaled; palpus porrect, narrow, fringed below with long scales; pectus and femur with long, hairlike scales. FW light orange from base to distal end of DC, charcoal gray beyond (Figs. 26, 27); orange region with diffuse, black longitudinal lines along veins, surrounded on anterior, posterior, and distal margins by a black border; HW (Figs. 26, 27) with a light orange central region extending from base to slightly beyond DC, iridescent purple-black merging to charcoal gray beyond; cubital



FIGS. 26-36. Adults of Josiini (life size). 26, *Thirmida discinota*, male; 27, *T. discinota*, female; 28, *Josia radians*, male; 29, *J. radians*, female; 30, *Josia gopala*, male; 31, *J. gopala*, female; 32, *Josia turgida*, male; 33, *J. turgida*, female; 34, *Josia aurifusa*, male (dark form from Puente Victoria); 35, *J. aurifusa*, male; 36, *J. aurifusa*, female. Photograph by Cal Snyder.

vein thinly lined with black scales; a small, black spot on upper discocellular cross vein. Upper and lower wing surfaces the same, except veins below uniformly orange rather than black.

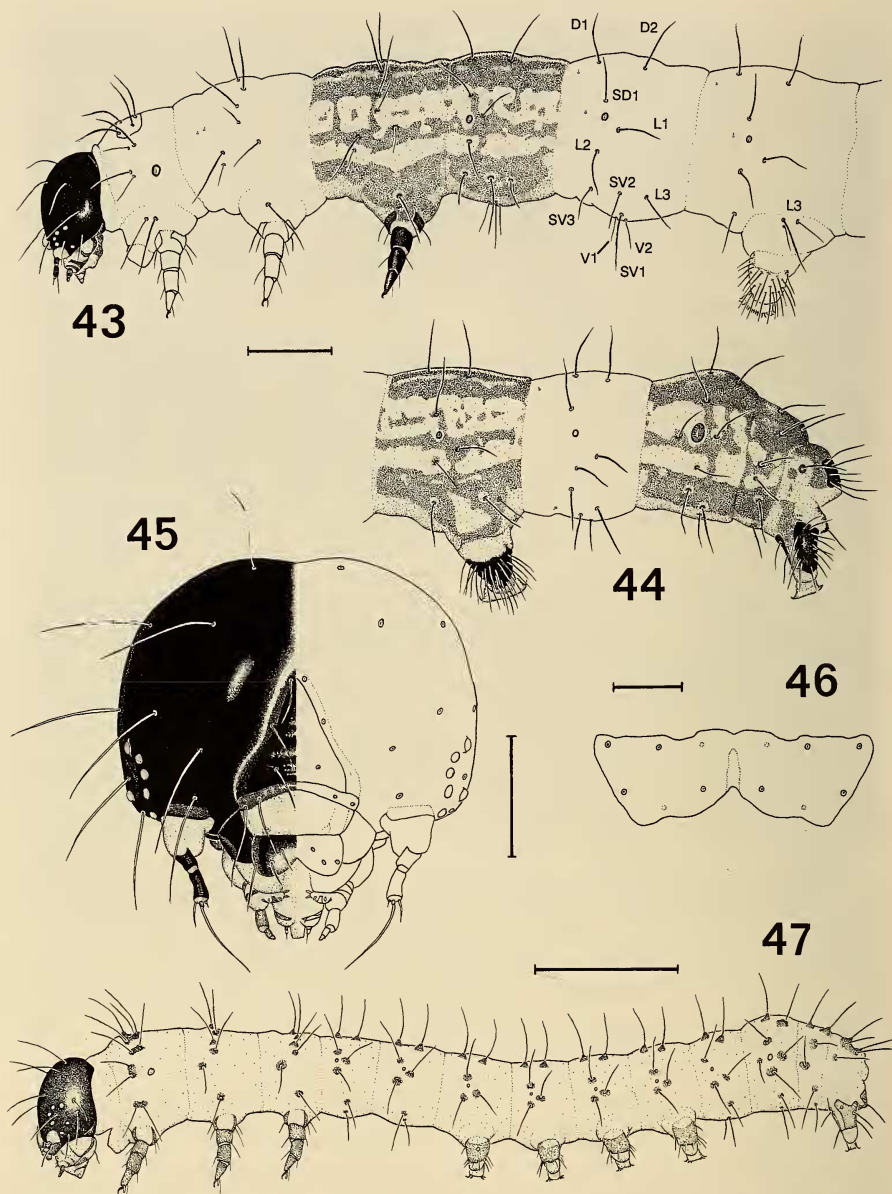
Discussion. Warren (1900) described *discinota* in the genus *Scea*, which was at that time placed in the Cyllopodinae (Geometridae). His description was based on a single female specimen (BMNH). Warren's taxon was transferred to *Thirmida* in the Dioptinae by Prout (1918),



FIGS. 37-42. Collecting sites for *Josiini* (all in the State of Mérida, Venezuela). 37, Paseo Los Pinos (1450 m), a locality for *Josia radians*; 38, Along the road from Estanques to Páramo Las Coloradas (1150 m), a locality for *J. radians*; 39, Las Playitas, near Bailadores (2250 m), a locality for *J. radians* (the foliage and flowers at left are those of *Passiflora manicata*); 40, Cloud forest margin (2300 m) in Monterrey, a locality for *J. gopala*; 41, Puente Victoria (540 m), a locality for *J. aurifusa*; 42, La Caña on the road from El Valle to La Culata (2420 m), northwest of the city of Mérida, a locality for *Thirmida discinota*. Photographs by L. Daniel Otero.

who considered *discinota* to be a subspecies of *T. dimidiata* Walker. This arrangement was followed by all subsequent authors (Hering 1925, Talbot 1929, Bryk 1930). We compared specimens of *T. dimidiata* from Bogotá, Colombia, the type locality (Walker 1854:466), with our Mérida material, and discovered numerous differences in wing pattern and genitalia. We therefore recognize the two as distinct, hereby returning *Thirmida discinota* to species level status.

Thus we recognize six species in *Thirmida*, five of which are figured in Hering (1925: plate 71). The only one with which *T. discinota* could be confused is *T. dimidiata*. Adults may be separated on the basis of



FIGS. 43-47. Larval stages of *Thirmida discinota*. 43, Head, thorax, and segments A1-A3 of fourth instar, lateral view (scale line = 2 mm); 44, Segments A6-A10 of fourth instar, lateral view (scale line = 1 mm); 45, Head of fourth instar, frontal view (scale line = 1 mm); 46, Prothoracic shield of fourth instar, dorsal view (scale line = 1 mm); 47, First instar, lateral view (scale line = 1 mm). [See Figs. 52-56 for key to symbols.]

wing pattern: the orange in the forewing of *T. dimidiata* extends beyond the distal margin of the discal cell, while in *T. discinota* it stops at the end of the discal cell (Figs. 26, 27).

This life history description is the first for a member of *Thirmida*. Adults and immatures of the other species, known from the Andes of Colombia and Ecuador at elevations between 1200 and 2300 m, will likely be discovered by collecting in habitats similar to that of *T. discinota*. Hering (1925), noting wing pattern similarities, suggested that the closest relatives of *Thirmida* are the Andean genera *Scea* and *Cyanotricha*.

Mimicry occurs throughout the Diptinae (Seitz 1925, Köhler 1930). In his description of the new genus and species *Thermidarctia thermidoides* in the Pericopinae (Arctiidae), Talbot (1929) noted what he called an "almost perfect resemblance" (p. 133) between his taxon and *Thirmida discinota*. Mérida is the type locality for both moths.

Josia radians Warren, 1905a

Distribution. Bryk (1930) reported *J. radians* from Mexico to Colombia, Guyana, and Venezuela, presumably based on museum specimens. However, *J. radians* frequently is confused with *J. ligata* Walker (type locality Bogotá, Colombia) and *J. frigida* Druce (type locality Las Mercedes, Guatemala). In all probability, the majority of material that Bryk examined was misidentified.

Reliably determined museum material, and specimens we have collected, suggest that the species occurs from the State of Aragua, Venezuela west to the Colombian border. It probably occurs in eastern Colombia as well. Although there is no locality data on the holotype, Warren's (1905a) description of *J. radians* gave the following: "1 male from Onaca, Sta. Martha, 2200 ft., wet season, September-October 1901 (Engelke)." We have been unable to locate this site, but assume that it is a misspelling of Ocaña, a locality in the eastern Cordillera of Colombia near the Venezuelan border (Fig. 1).

Collecting Localities. Eggs, larvae, and adults of *Josia radians* were collected at eight different localities (Figs. 37-39, 72). There were seven sites in the state of Mérida, and an eighth locality in the Parque Nacional Henri Pittier, State of Aragua. Elevations ranged from 1100 m (near El Amparo) to 2250 m (Las Playitas, near Bailadores). These collecting sites cover a variety of life zones (PM-mf, PM-wf, PM-df) and vegetation types. They include cloud forest (Henri Pittier), as well as highly disturbed habitats such as a coffee plantation (La Mucuy) and a small patch of *Passiflora* on the road margin in agricultural land (Las Playitas). In one case (Paseo los Pinos near the city of Mérida), *J. radians* im-

maturation were found on their host in a vacant lot within a residential area.

The species seems to occur throughout the year; our collecting dates include the months of May, June, July, September, October, and December of 1992, as well as February and March of 1993.

Foodplant. We collected *Josia radians* on four *Passiflora* species. It was most frequently found on *P. capsularis* L. (subgenus *Plectostemma*), a widespread species that occurs from Guatemala south to central Brazil and Paraguay up to 1900 m, and throughout the Greater Antilles. At Las Playitas (Fig. 39), the highest elevation so far known for *J. radians* (2250 m), larvae were collected on *Passiflora manicata* Jussieu (subgenus *Granadillastrum*). This plant is known from western Venezuela east to Colombia and south to northern Peru between 1500 and 2500 m elevation. The third *Passiflora* used by *J. radians* is *P. cuneata* (subgenus *Plectostemma*), one of the hosts for *Josia gopala* (see below). Eggs of *J. radians* also were found on *P. rubra* L. (subgenus *Plectostemma*). *Passiflora rubra* is widespread, occurring throughout the West Indies, from Venezuela and Colombia south to Bolivia, and in eastern Brazil. *Passiflora rubra* and *P. capsularis* are close relatives and difficult to distinguish (Killip 1938, Holm-Nielsen 1988, Vanderplank 1991). Our identifications were confirmed by comparison of flowers and fruits.

Egg. Diameter = 0.91–0.98 mm ($n = 12$). Eggs are laid singly. Duration: 7 to 8 days. Development time from egg to adult = 40–45 days.

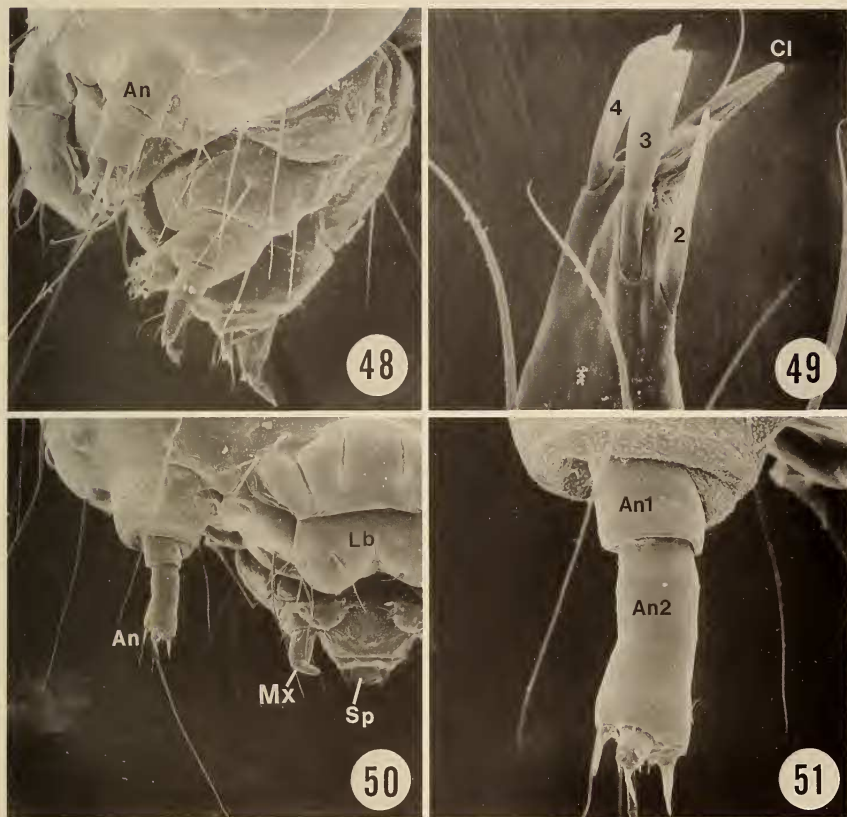
First Instar. Head entirely black, except clypeus white. First instars of *J. radians* differ from the other species we studied in the following: antennal segments 1 and 2 short (Fig. 48); thoracic legs with tarsal setae elongate, apex of TS3 emarginate (Fig. 49); thorax with a red dorsal patch on T2 (Fig. 56); segments A1, A3 and A8 ringed with reddish, segments A5 and A10 with a red dorsal patch, A7 with a red lateral patch below spiracle (Fig. 56). Body length = 5.73–6.01 mm ($n = 3$); head width = 0.54–0.57 mm ($n = 6$).

Second and Third Instars. Similar in color and setal pattern to final instar. Head widths: 2nd = 0.90–0.91 mm ($n = 6$); 3rd = 1.40–1.44 mm ($n = 6$).

Final (Fourth) Instar. Head shiny black with white front, wide white regions extending along ecdysial lines down to antenna, and a pair of lateral white stripes, each from vertex to stemmata, widening below (Fig. 54); antenna with segment 2 approximately twice the length of segment 1 (Fig. 51). Prothoracic shield with anterolateral angles produced, an unpigmented medial seam (Fig. 55); ground color of thorax and abdomen reddish maroon, with a complex white and yellow pattern overlying it (Fig. 16); lateral and dorsal light-colored areas reticulate (Figs. 52, 53); venter entirely white; dorsal red portions more heavily pigmented in an alternating pattern on segments T2, A1, A3 and A5; segment A9 conspicuous, entirely white above (Figs. 16, 53). Tarsal setae (Fig. 57) similar to *Thirmida discinota*. Pattern of primary setae on thorax and abdomen (Figs. 52, 53) similar to *J. aurifusa* and *J. turgida*; lateral plate of A10 proleg base with approximately 9 setae. Body length = 28–30 mm; head width = 2.13–2.22 mm ($n = 5$).

Pupa. Cremaster (Figs. 58–60) conical, with a row of longitudinal striae circling base and two more distal concentric rings of reticulate striae; eighth stout, hook-shaped setae. The pupal stage lasted 14 days.

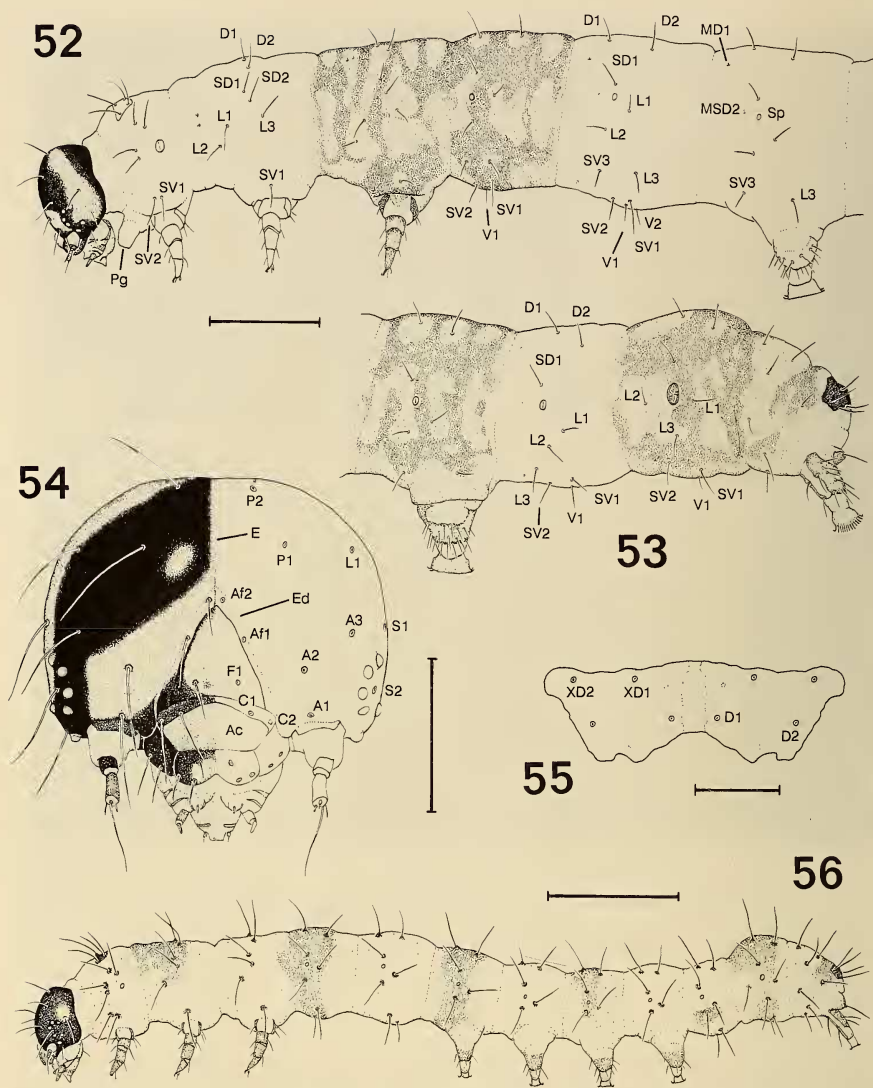
Adult. FW length = 16.0–19.0 mm. Head orange-yellow with vertex, antenna and scales behind eye black; pectinations of male antenna moderately long; labial palpus



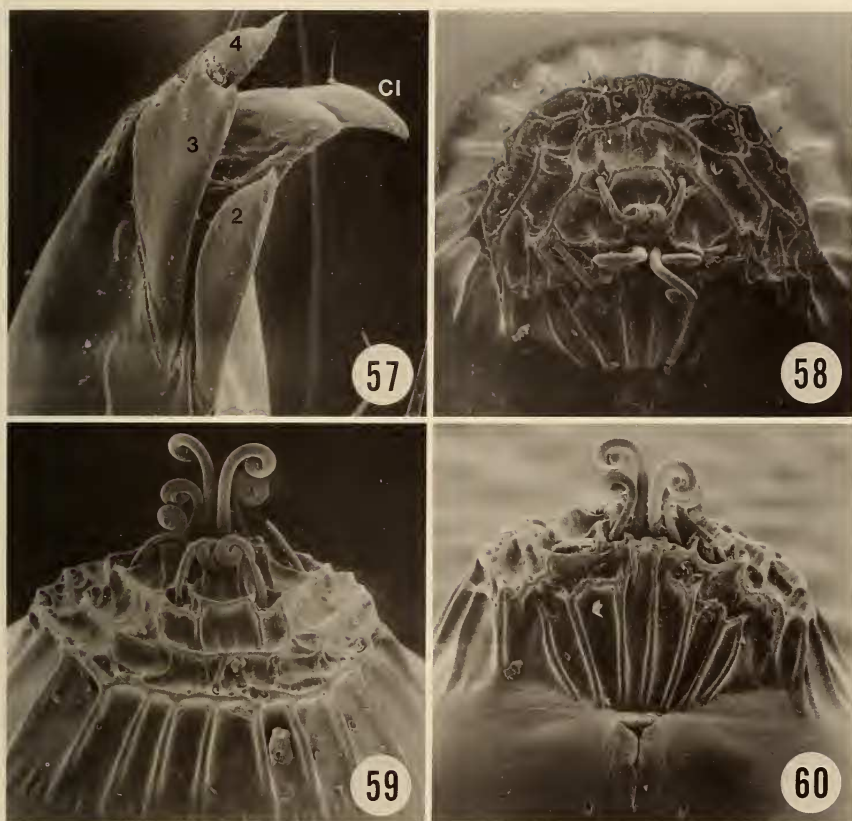
FIGS. 48-51. Scanning electron micrographs of *Josia radians* larvae. **48**, Ventral portion of first instar head, lateral view ($\times 254$); **49**, Tarsus of right metathoracic leg of first instar, mesal view, showing tarsal setae ($\times 800$); **50**, Ventral portion of fourth instar head, frontal view of right side ($\times 68$); **51**, Right antenna of fourth instar, frontal view ($\times 200$). [An = antenna; Cl = tarsal claw; Lb = labrum; Mx = maxillary palpus; Sp = spinneret; 2, 3, 4 = tarsal setae 2, 3, and 4.]

porrect, exceeding front; palpus relatively wide, segment 1 yellow, segment 2 black with yellow scales on venter, segment 3 black. Dorsum of thorax black with orange-yellow stripe on each side running from patagium to abdomen; tegula black in lateral half, yellow along mesal half, with fringe of long yellow scales distally; lateral portions of thorax mostly black, orange-yellow below wing bases; legs black, buff scales on dorsal surfaces; anterior surfaces of forecoxa light buff. FW and HW (Figs. 28, 29) black with thin, longitudinal orange-yellow stripe from base to within 1 mm of outer margin, stripe slightly wider in female; FW and HW costa orange-yellow from base to approximately two thirds out; HW anal margin orange-yellow; longitudinal stripe of FW wider and more diffuse below. Abdomen black with orange-yellow lateral stripe on each side, stripe becoming gray at caudal margin of A8; venter of abdomen whitish buff.

Discussion. The moths we reared match the male holotype of *Josia radians* Warren (BMNH) in wing pattern and genitalic morphology.



FIGS. 52-56. Larval stages of *Josia radians*. 52, Head, thorax, and segments A1-A3 of fourth instar, lateral view; 53, Segments A6-A10 of fourth instar, lateral view (scale line = 2 mm); 54, Head of fourth instar, frontal view (scale line = 1 mm); 55, Prothoracic shield of fourth instar, dorsal view (scale line = 0.5 mm); 56, First instar, lateral view (scale line = 1 mm). [A = anterior seta; Af = adfrontal seta; C = clypeal seta; E = epicranial suture; Ed = ecdysial line; F = frontal seta; MD = dorsal proprioceptor seta; P = posteriodorsal seta; Pg = prothoracic gland; S = stemmatal seta; Sp = spiracle; XD = XD seta; for other symbols see "Methods."]



FIGS. 57-60. Scanning electron micrographs of immature stages of *Josia radians*. 57, Tarsus of right T3 leg of fourth instar larva, mesal view, showing tarsal setae 2, 3, and 4 ($\times 358$); 58, Cremaster, posterior view ($\times 69$); 59, Cremaster, dorsal view ($\times 73$); 60, Cremaster, ventral view ($\times 71$). [Cl = tarsal claw.]

However, *J. radians* belongs to a group of closely related species that includes *J. ligata* Walker, *J. frigida* Druce, and *J. fustula* Warren. Identifications in this complex are extremely difficult (Forbes 1931).

Josia gopala Dognin, 1891

Distribution. *Josia gopala* is known only from the State of Mérida, Venezuela (AMNH, BMNH, MIZA, NMNH, ZMH). The locality label on the female holotype (NMNH) reads "Mérida, Venezuela; Terre Temperee," the latter (in French) probably referring to a temperate habitat. Based on museum label data and on data we have accumulated, *Josia gopala* occurs within a fairly restricted altitudinal range, between 2000 and 3000 meters. Although *J. gopala* is rare in museum collections,

previously known from less than 20 specimens, the moth can be quite common in Mérida.

Collecting Localities. Eggs and larvae were collected at four cloud forest localities. Two sites, close together in Asentamiento Monterrey, El Valle (LM-mf) at 2300 and 2350 m elevation, were visited on 14 and 23 June 1992, 16 August 1992, and 7 March 1993. One of these is along a cloud forest margin bounded by agricultural land and dispersed human habitations (Fig. 40), while the other is in a pine plantation in what was formerly cloud forest. Our other two sites were along the road to El Morro (2150 m), visited on 6 September 1992 (LM-mf), and in Parque Nacional Sierra Nevada, La Mucuy (2300 m), visited on 12 October 1992 (LM-wf). The species seems to be restricted to the borders of forested habitats.

Foodplant. *Josia gopala* was discovered feeding on two *Passiflora* species. Eggs were collected on *Passiflora cuneata* Willdenow (subgenus *Plectostemma*) growing in the shaded forest margins. This *Passiflora* is known from the mountains of central Venezuela east to the Cordillera Santa Marta and eastern Cordillera of Colombia at elevations between 700 and 3800 m. Caterpillars also were found on *Passiflora gritensis* Karsten (subgenus *Granadilla*). In one case, the *P. gritensis* plants were growing in a pine plantation. *Passiflora gritensis* is known only from western Venezuela at altitudes near 2500 m. These two *Passiflora* species occur together at the Monterrey sites. Females of *J. gopala* tend to oviposit on tender, lower leaves of the host near the ground, especially on the leaves of seedlings or new shoots.

Egg. Diameter = 0.86–1.01 mm ($n = 18$). Duration: 7 to 8 days. Eggs are laid individually, not in clusters. Development time from egg to adult = 52–56 days.

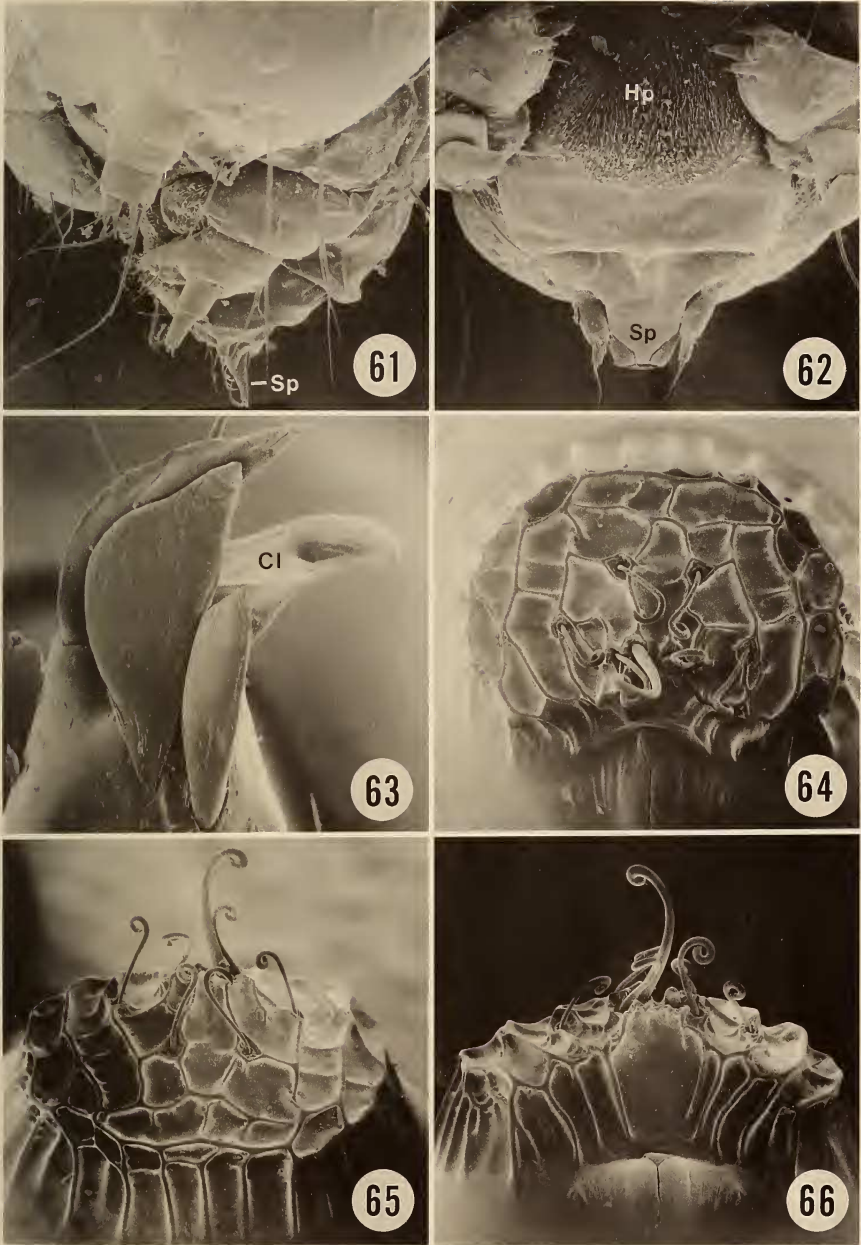
First Instar. Head dark brown except for white clypeus, and small light brown patches at ventral angles of front beyond ecdysial lines. General morphology and primary setae (Figs. 61, 71) similar to other Josiini. Body length = 4.38–5.19 mm; head width = 0.57–0.62 mm.

Second and Third Instars. Similar in pigmentation and setal pattern to final instar. Head widths: 2nd = 0.89–0.95 mm; 3rd = 1.39–1.50 mm ($n = 4$).

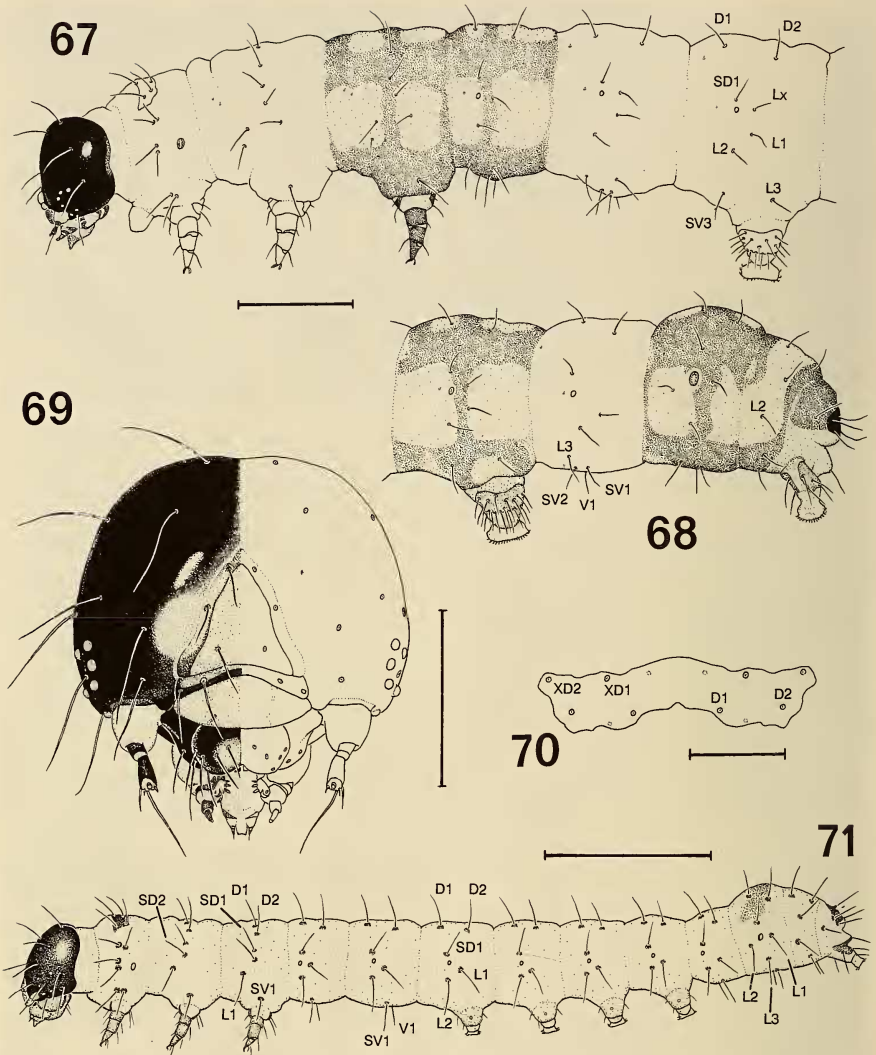
Final (Fourth) Instar. Head shiny black except for white frons and clypeus, and two ovoid white patches on either side of ecdysial lines (Fig. 69); antenna with segment 2 approximately twice the length of segment 1. Prothoracic shield narrow, no medial seam (Fig. 70); ground color of thorax and abdomen reddish maroon, overlying pattern simple, white and yellow (Fig. 17); light-colored lateral and dorsal areas roughly rectangular in shape (Figs. 67, 68); venter entirely white; segment A9 conspicuous, entirely white above. Tarsal setae (Fig. 63) with TS2 lanceolate, TS3 broad and leaf-shaped, TS4 sword-shaped with apex acute. Setal pattern on T1–A10 (Figs. 67, 68) similar to last instars of other *Josia* species except: a novel L seta (seta "Lx" in Fig. 67) present on segments A2–A6, located between SD1 and L1; lateral plate of A10 proleg base with only 4 setae ($n = 9$ in other *Josia* species). Body length = 25–26 mm; head width 1.9–2.13 mm ($n = 5$).

Pupa. Cremaster (Figs. 64–66) short, somewhat flattened distally, fluting irregular; eight delicate, widely spaced, hook-shaped setae. Duration: approximately 19 days. The pre-pupal larvae weave a shelter of leaves and crawl into it to pupate (2 observations).

Adult. FW length = 16.5–17.5 mm. Head, thorax, and abdomen dark charcoal blue-



FIGS. 61-66. Scanning electron micrographs of immature stages of *Josia gopala*. **61**, Ventral portion of first instar head, lateral view ($\times 294$); **62**, Maxillary and hypopharyngeal complexes of fourth instar larva, frontal view ($\times 215$); **63**, Tarsus of right prothoracic leg of fourth instar larva, mesal view ($\times 468$); **64**, Cremaster, posterior view ($\times 81$); **65**, Cremaster, dorso-posterior view ($\times 76$); **66**, Cremaster, ventral view ($\times 81$). [Cl = tarsal claw; Hp = hypopharynx; Sp = spinneret.]



FIGS. 67-71. Larval stages of *Josia gopala*. **67**, Head, thorax, and segments A1-A3 of fourth instar, lateral view; **68**, Segments A6-A10 of fourth instar, lateral view (scale line = 2 mm); **69**, Head of fourth instar, frontal view (scale line = 1 mm); **70**, Prothoracic shield of fourth instar, dorsal view (scale line = 0.5 mm); **71**, First instar, lateral view (scale line = 1 mm). [Lx = novel L seta; see text.]

gray, a lighter lateral stripe on each side of abdomen; pectinations of male antenna short; labial palpus narrow and porrect, slightly exceeding front. Wings (Figs. 30, 31) with outer margins dark bluish black. FW with a wide, yellow longitudinal stripe extending from base to fork of M_3 and $CuA1$, just beyond DC; posterior margin light gray below; costa black; HW with large yellow central area; anterior margin light gray above; dorsal and ventral wing surfaces with essentially the same pattern.

Discussion. The species *gopala* was described by Dognin (1891) in *Flavinia*, a genus in the Geometridae (Watson et al. 1980), but was moved by Prout (1918) to *Josia*. The moth can be separated from most other *Josia* by the wide, truncate, longitudinal FW stripe which extends for only two thirds the wing length (Figs. 30, 31; Hering 1925). The larva exhibits a relatively simple pattern, with roughly rectangular, yellow and white patches on each segment laterally and dorsally (Fig. 17). The last instar is unique among the known species of Josiini in its possession of an extra L seta on segments A2–A6 (Figs. 67, 68).

Based on similarities of wing pattern (Forbes 1931) and genitalia (JSM, unpubl.), the closest relatives of *Josia gopala* are *J. patula* Walker and *J. gephyra* Hering. These two are slightly larger species (FW length = 18.5–21.0 mm) with the yellow forewing stripe narrower and extending further out (Hering 1925). *Josia patula* is fairly well represented in museum collections, being known from Choachi, Villavicencio, and Bogotá, Colombia (BMNH, CMNH, CUIC, NMNH, ZMH). *Josia gephyra* is rare; we have seen only four specimens (NMNH, BMNH), all collected at the type locality, Cañon del Monte Tolima, Colombia. This is a high altitude site; one of these specimens was caught at 4700 m (BMNH). Assuming the label is correct, this is the highest altitude recorded for any species of Dioprinae.

Josia aurifusa Walker, 1854

Distribution. *Josia aurifusa* appears to be endemic to Venezuela, occurring from the state of Aragua west to Tachira (AMNH, CMNH, MIZA, MNHN). The label on the male holotype (BMNH) gives the locality simply as "Venezuela."

Collecting Localities. We collected eggs, larvae, and adults of *Josia aurifusa* at two localities in the Parque Nacional Henri Pittier (PM-wf) in the State of Aragua. On 22 March 1992, we collected six eggs on *Passiflora* leaves at Rancho Grande Field Station (1100 m). We also collected 16 eggs and one final instar larva on 2 April 1992, near a stream crossing the road from Maracay to Choroni (860 m) on the northern slope of the mountains (Fig. 73). An adult female, collected at the second locality, produced eight eggs from which reared material was obtained. Eggs of the species also were collected at a third locality on the road from Barinas to Santo Domingo at Quebrada El Alambique (1250 m; also PM-wf) in the State of Barinas. All three are cloud forest sites. Eggs and larvae of what turned out to be an extremely dark form of *Josia aurifusa* (Fig. 34) were found in the state of Mérida at Puente Victoria (540 m, T-mf) on the road from Mérida to El Vigía (Fig. 41).

Foodplant. *Josia aurifusa* was found on two *Passiflora* species. At the Aragua localities it fed on *P. rubra*, while at Puente Victoria it was on *P. capsularis*. Both plant species are discussed under *J. radians* (above).

Egg. Diameter = approximately 0.7–0.8 mm; laid either singly or in small clusters of up to nine eggs. Duration: 4–5 days. Development time from egg to adult = 59 days.

First Instar. Head dark brown, slightly lighter on front, antenna short (Fig. 79); body lacking pigment (Fig. 78). Body length = 4.11 mm ($n = 1$); head width = 0.49–0.51 mm ($n = 5$).

Second and Third Instars. Similar in markings and setal pattern to final instar. Head widths: 2nd instar = 0.82–0.83 mm; 3rd instar = 1.25–1.30 mm ($n = 5$).

Final (Fourth) Instar. Head white, with wide, brownish black frontolateral stripes extending from stemmata up to epicranial suture, stripes widening near suture (Fig. 76); labrum black with a white central region; antenna (Figs. 80, 81) with segment 2 relatively short, less than twice the length of segment 1. Prothoracic shield (Fig. 77) with an unpigmented medial seam, anterolateral angles produced, curled inward; ground color of thorax and abdomen reddish maroon (Fig. 18), red colored regions lightly spotted with white; yellow-white dorsal and lateral patches irregularly shaped (Figs. 74, 75), roughly rectangular, relatively small (compared to *J. turgida*, below); seta L3 on A3–A6 surrounded by a smallish white spot (Fig. 75); venter white with red, transverse connecting lines on A1 and A2; segment A9 conspicuous, entirely white above (Fig. 18). Tarsal setae as in *Josia gopala*. Primary setae (Figs. 74–76) as in *Josia radians*; lateral plate of A10 proleg base with approximately 9 setae. Body length = 24.5–26.0 mm; head width = 1.86–1.98 mm ($n = 6$).

Pupa. Cremaster blunt, with uneven longitudinal flutes at base and irregular striae on distal flattened portion; strongly concave ventrally; eight hook-shaped setae present. Duration: 10 days.

Adult. FW length = 13.5–17.0 mm. Antenna black; head mostly black, face white with front blackish gray; scales at antennal base white; pectinations of male antenna moderately long; labial palpus porrect, relatively long and thin, extending well beyond front; basal three fourths of palpus segment 1 white, rest of palpus black. Dorsum of thorax black, an orange stripe on each side running from patagium to base of abdomen; tegula orange, black at base; lateral portions of thorax orange; coxa black laterally, white on anterior surfaces; legs dark gray, tibiae whitish-buff below. FW black with a wide, orange longitudinal stripe from base to within 2 mm of outer margin (Figs. 35, 36), stripe tapering gradually toward apex; Rs entirely black through orange stripe; HW (Figs. 35, 36) black with caudal two thirds orange; orange region with a diffuse, black, wedge-shaped streak along vein 2A from near base, widening toward outer margin; costa of HW light orange in basal two thirds. Abdomen black with wide, orange lateral stripes, stripes becoming buff at caudal margin of A8; venter white. HW almost entirely black in some specimens (Fig. 34), with a diffuse orange streak along CuA2, and anal margin a combination of orange and black scales.

Discussion. Walker's description of *aurifusa* (1854: 293) and the holotype (BMNH) match our material from Choroní. However, *Josia aurifusa* is a variable species (Hering 1925); our specimens from Puente Victoria are extremely dark (Fig. 34). Four names have been synonymized with *aurifusa*, all of which currently stand as either forms or aberrations (Bryk 1930). The phenotypes associated with these names vary in the shape of the longitudinal forewing stripe and in the amount of black in the hind wing. We recognize one of those, "form" *turgida* Warren, as a distinct species (see below).



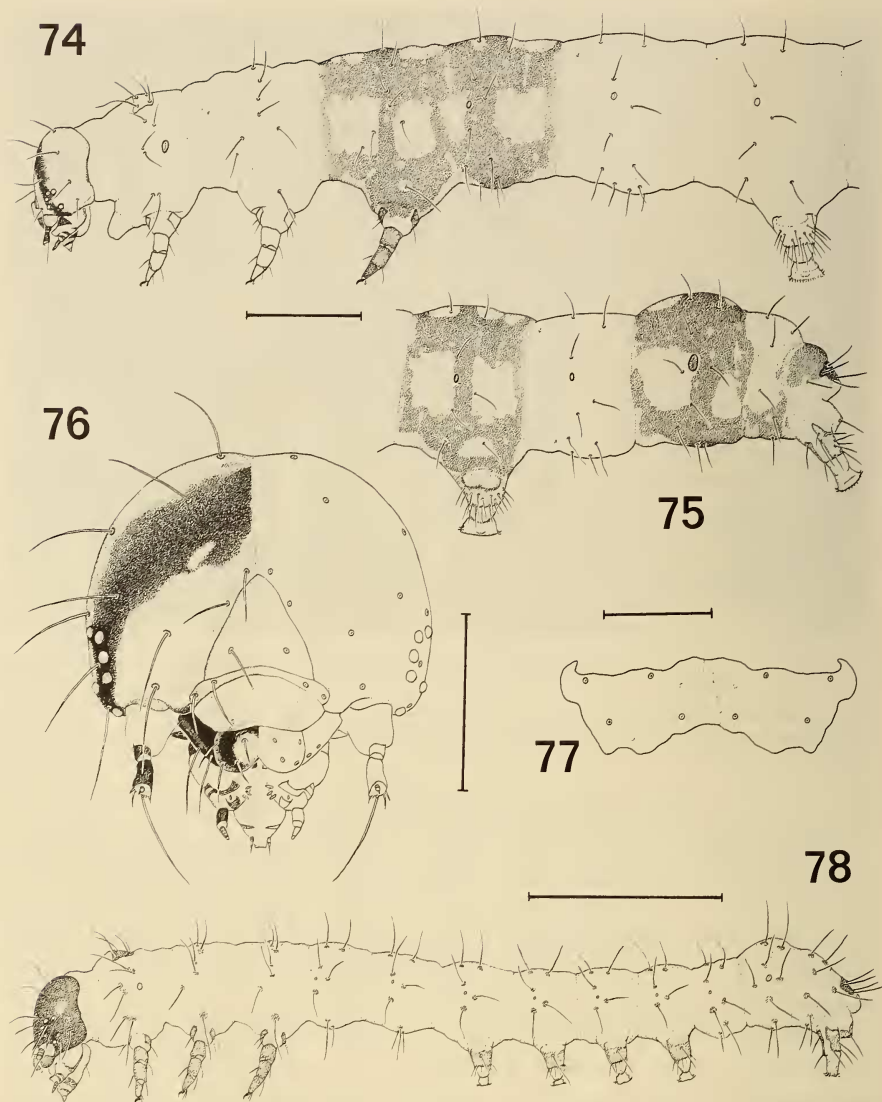
FIGS. 72, 73. Collecting sites for *Josia* species. **72**, Beside the road to La Mesa de Ejido, State of Mérida, 1.8 km from the turnoff in the Panamerican Highway on the way to Jaji (1560 m), a locality for *Josia radians*; **73**, Along the road from Maracay to Choroni (860 m), State of Aragua, a locality for *Josia aurifusa*. Photographs by L. Daniel Otero.

Josia turgida Warren, 1905b, revised status

Distribution. Like *Josia aurifusa*, *J. turgida* appears to be endemic to Venezuela. The species is sympatric with *J. aurifusa*, but it has been recorded from further east (Puerto la Cruz, Anzoátequi; CMNH), and does not seem to extend as far west; our western-most record is Altamira in the state of Barinas (LDO, collector). The type locality is Valencia, Venezuela (State of Carabobo).

Collecting Localities. Eggs and first instar larvae of *Josia turgida* were found along the road to Altamira in the State of Barinas, approximately 2.6 km from the turnoff on the Barinas to Santo Domingo road (645 m; T-mf). Eleven eggs were collected on 28 June 1992, and 14 eggs and five first instar larvae on 13 September 1992. Eggs of the species also were collected on the road from Barinas to Santo Domingo at Quebrada El Alambique (1250 m) in the State of Barinas.

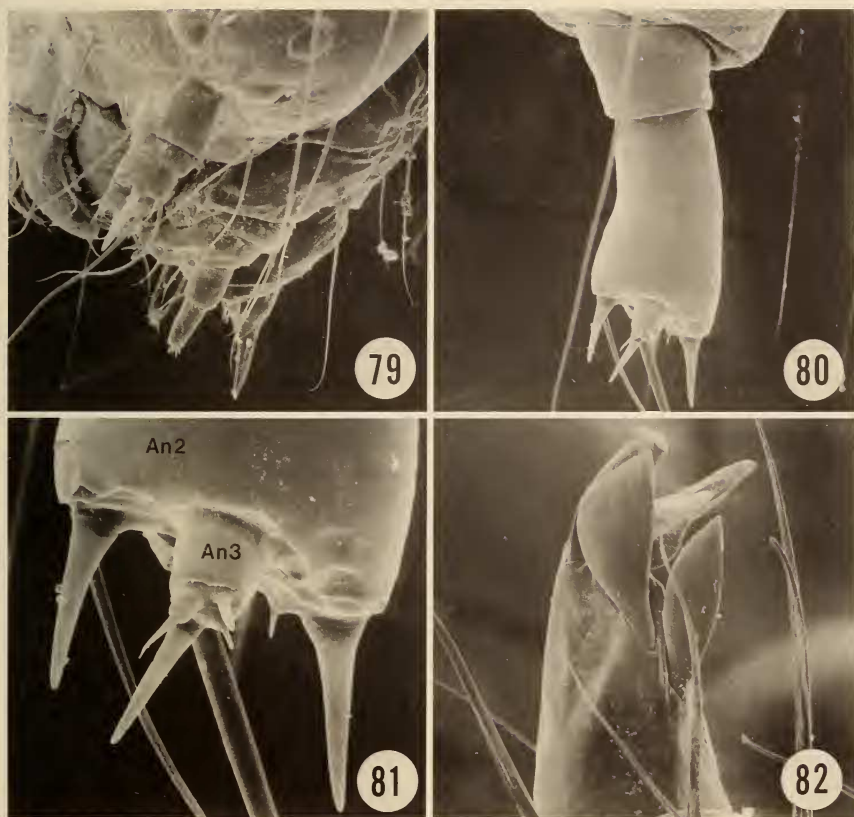
Foodplant. The known hostplants are *Passiflora capsularis* and *P. rubra*. These *Passiflora* species also are used by *J. aurifusa* and *J. radians*. Larvae were collected from plants growing in secondary vegetation along road margins.



FIGS. 74-78. Larval stages of *Josia aurifusa*. 74, Head, thorax, and segments A1-A3 of fourth instar, lateral view; 75, Segments A6-A10 of fourth instar, lateral view (scale line = 2 mm); 76, Head of fourth instar, frontal view (scale line = 1 mm); 77, Prothoracic shield of fourth instar, dorsal view (scale line = 0.5 mm); 78, First instar, lateral view (scale line = 1 mm).

Egg. Diameter = 0.7 to 0.8 mm; found in small clusters of two to nine eggs. Duration: 4 days. Development time from egg to adult = 42 days.

First Instar. Similar to other *Josini*; head dark brown, slightly lighter on front. Body length = 4.05 mm; head width = 0.48 mm (n = 1).

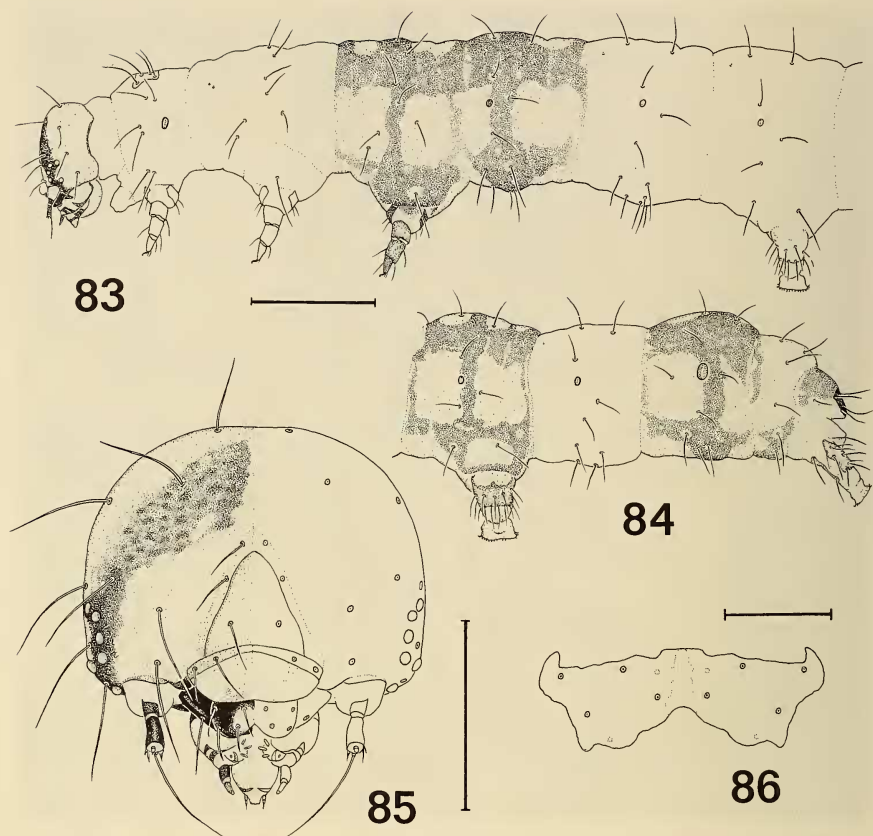


FIGS. 79–81. Scanning electron micrographs of *Josia aurifusa* larvae. **79**, Ventral portion of first instar head, lateral view ($\times 350$); **80**, Right antenna of fourth instar, frontal view ($\times 266$); **81**, Distal portion of fourth instar antenna showing segments 2 and 3 ($\times 734$). [An = antennal segment.]

FIG. 82. Right tarsus on T2 of fourth instar *Josia turgida* larva, mesal view ($\times 292$).

Second and Third Instars. Similar in coloring and setal pattern to final instar. Head widths: 2nd instar = 0.81–0.83 mm; 3rd instar = 1.22–1.26 mm ($n = 5$).

Final (Fourth) Instar. Head (Fig. 85) white with wide, brown, irregularly patterned frontolateral stripes extending from stemmata up to epicranial suture, stripes widening near suture; labrum black with a white central region; antenna with segment 2 relatively short, less than twice the length of segment 1. Prothoracic shield with an unpigmented medial seam, anterolateral angles produced, curled inward (Fig. 86). Ground color of thorax and abdomen reddish maroon (Fig. 19); red colored regions lightly spotted with white (Figs. 83, 84); white spots present at bases of primary setae; yellow-white dorsal and lateral patches larger than in *J. aurifusa*, margins smoother; venter white, with red transverse connecting lines on A1 and A2; L3 on A3–A6 surrounded by a large white patch; segment A9 conspicuous, entirely white above (Fig. 19). Tarsal setae (Fig. 82) similar to *Josia gopala*. Primary setae (Figs. 83–85) as in *J. radians* and *J. aurifusa*; lateral plate of A10 proleg base with approximately 9 setae. Body length = 24.0–25.0 mm; head width = 1.88–1.94 mm ($n = 3$).



FIGS. 83-86. Larval stages of *Josia turgida*. **83**, Head, thorax, and segments A1-A3 of fourth instar, lateral view; **84**, Segments A6-A10 of fourth instar, lateral view (scale line = 2 mm); **85**, Head of fourth instar, frontal view (scale line = 1 mm); **86**, Prothoracic shield of fourth instar, dorsal view (scale line = 0.5 mm).

Pupa. Cremaster similar to *J. aurifusa*, slightly less concave ventrally; eight hook-shaped setae present. Duration: approximately 17 days.

Adult. FW length = 14.0-17.0 mm. Head and antenna black; face white with front blackish gray; scales at antennal base white; pectinations of male antenna moderately long; labial palpus porrect, relatively long and thin, extending well beyond front; basal three fourths of segment 1 white, rest of palpus black. Dorsum of thorax black, an orange stripe on each side running from patagium to base of abdomen; tegula mostly orange, black at base; lateral portion of thorax orange; coxa black on lateral surface, white on anterior surface; legs dark gray, tibiae whitish-buff below. FW black with a wide, orange longitudinal stripe from base to within 2 mm of outer margin (Figs. 32, 33); stripe tapered, slightly irregular along anterior margin near apex; Rs black at base, orange beyond; HW (Figs. 32, 33) orange with upper angle black from a point near upper corner of DC to outer margin; a diffuse black patch along 2A near outer margin. Abdomen black with wide, orange lateral stripes, stripes becoming buff at caudal margin of A8; venter white.

Discussion. *Josia turgida*, described by Warren (1905b:314) in the subfamily Cylopodinae (Geometridae), was considered a form of *J. aurifusa* by Hering (1925) and subsequent authors, but we here elevate it to species status.

Although *J. turgida* and *J. aurifusa* are extremely close, we found what seem to be reliable differences between these two sympatric species. Adults of *J. turgida* generally are more orange than those of *J. aurifusa* (compare Figs. 32–36). The FW stripes are wider and the black portion of the HW does not reach the wing base. In *J. turgida* there is usually a prominent orange macula on the dorsum of the mesothorax, while in *J. aurifusa* this area is either entirely black, or has a very small, faint orange spot. There are also subtle differences between the larvae. The yellow-white lateral patches on the thorax and abdomen are larger in *J. turgida* than in *J. aurifusa* (compare Figs. 74, 75 with 83, 84), especially those surrounding seta L3 on the proleg-bearing segments. The head stripes of *J. turgida* are lighter in color, and the pigmentation is more irregular (Fig. 85). The larvae of *J. turgida* are thus generally lighter in color than those of *J. aurifusa*.

Josia aurifusa and *J. turgida*, together with their various color forms, belong in a species complex with *Josia auriflua* Walker, known from the western Andes of Colombia south to Bolivia. To further complicate matters, three Dognin names—*inaequiflexa*, *scalata*, and *flavipars*—are listed as subspecies of *J. auriflua* in Bryk (1930). The entire *aurifusa* complex poses a serious taxonomic challenge; wing pattern variation seems to merge, and genitalic differences are not always clear-cut (JSM, unpubl.).

CONCLUSIONS

Based on our findings for these five Venezuelan Josiini and on published reports for other taxa, we now can offer a general summary of biological characteristics for the tribe.

The species occur over a wide range of elevations, from lowland jungle to shrubby, high altitude sites in the Andes of South America and the Central Cordillera of Central America. *Cyanotricha bellona* has been recorded at 4000 m in Peru (BMNH), and *Josia gephyra* was collected in Colombia at 4700 m (see discussion of *J. gopala* above). Josiini are most common in secondary forests and disturbed habitats, but they also occur in pristine environments. Even in primary forests, however, they seem to favor light gaps, forest edges, and stream margins, perhaps due to the higher frequency of their passifloraceous hosts in such habitats. In this study, immatures of *Josia radians* were found on *Passiflora* growing in a coffee plantation, and at another site close to the city of Mérida within the confines of a housing development.

At least one species is of economic importance. *Cyanotricha necyria* is an occasional pest in commercial fields of *Passiflora mollissima* in the Andes of Colombia, Ecuador, and Peru (Castaneda 1956, Martin & Nakasone 1970). Markin et al. (1989) have studied *C. necyria* and other Josiini as potential biological control agents of *P. mollissima*, a damaging weed in Volcano National Park, Hawaii.

Members of the Josiini share many life history features, some of which apparently are unique to the tribe. For example, unlike most Lepidoptera, which have either five or six larval instars, all Josiini so far studied have only four (Spitz 1931, d'Almeida 1932, Markin et al. 1989). The number of larval instars in other subfamilies of the Notodontidae is five (Packard 1895), and published reports for Dioptinae outside the Josiini indicate that five is typical there as well (Herbert 1920, Wolda & Foster 1978).

In the species we observed, and in *Cyanotricha necyria* (Markin et al. 1989), first instars often feed together on the same leaf, while subsequent instars feed individually. These observations agree with previous work showing this to be a general trend for the Notodontidae (Godfrey et al. 1989). Associated with this trend is a developmental change whereby the first instar mandibular margin is serrate, while that of later instars is smooth (Godfrey et al. 1989, Dockter 1993).

Josiini exhibit a characteristic pupation behavior. The pre-pupal caterpillar makes a shelter, using strong silk threads to weave pieces of leaves or debris together. The larva then pupates in this enclosure, normally within a few days after its construction. In the absence of such materials, the larva builds a flimsy silk net. Pupation usually takes place off the hostplant, but in one instance we found a pupa on its *Passiflora* host.

Several characteristics distinguish the immatures of Josiini from those of heliconiines, the only other Lepidoptera common on *Passiflora*. *Heliconius* eggs, deposited singly or occasionally in large clusters, are somewhat cylindrical with prominent surface sculpturing, and are usually yellow, orange, or red (Beebe et al. 1960, Benson et al. 1976, DeVries 1987). They are generally larger than the eggs of Josiini. Female Heliconiinae frequently oviposit on new leaves or on shoots near the meristem, whereas josiines tend to lay on older leaves closer to the ground, always on the leaf undersurface. The eggs of *Eueides* (Heliconiinae) are similar to those of Josiini in that they are frequently laid on the undersurface of mature leaves, and they are small and green. However, *Eueides* eggs differ in having prominent surface sculpturing (JSM pers. obs.).

Josiine larvae lack projections on the body. They exhibit the shagreened cuticle characteristic of other Dioptinae (Fracker 1915, Forbes

1939, Miller 1991), a trait that can be seen with the aid of a hand-lens. The caterpillars thus are impossible to confuse with heliconiine larvae, which are usually greenish white overlaid with various dark patterns, and which have long, spiny projections on the head, thorax, and abdomen (Beebe et al. 1960, Brown 1981, DeVries 1987).

Adult josiines can be recognized in the field by their erratic, fluttering flight and bright coloration. After landing first on the upper surface of a leaf, they often move quickly out of sight to the underside. Upon close examination, the unusual metathoracic tympanum and wing venation can be used as diagnostic features to distinguish them from all other Lepidoptera.

Having here described the immature stages of four *Josia* species and *Thirmida discinota*, we hope to discover life histories for still other taxa. We urge field workers collecting on or around *Passiflora* to learn to recognize and collect Josiini. A long-term goal is to accumulate enough hostplant data to compare patterns in the Josiini with those that have been described in the literature for the Heliconiinae (Benson et al. 1976). Because the immature stages appear to be a rich source of characters, their discovery also will benefit greatly systematic studies on the Dioprinae.

ACKNOWLEDGMENTS

We are grateful to INPARQUES (Instituto Nacional de Parques) for permission to collect in Venezuelan national parks. For permission to study at Rancho Grande, we thank Alberto Fernández Badillo, Director of the Estación Biológica Dr. Alberto Fernández Yépez. For help with defining life zones for our study sites, we thank José Remigio Guevara. Stephen Tillet provided identifications of *Passiflora* species. We also thank John MacDougal (Missouri Botanical Garden) and Christian Feuillet (Smithsonian Institution) for discussions concerning *Passiflora* identification and classification. Miguel Molinari helped with field work and additional *Passiflora* identifications, and Jorge Avila cared for moth cultures. For logistical help we would like to thank Alejandro Grajal and Stuart Strahl. David Wagner and Tim McCabe provided helpful comments on the manuscript. Cal Snyder kindly took the color photographs of adults.

We also would like to thank the following people and their institutions for the loan of adult material: Martin Honey and David Carter (BMNH); John Rawlins and Chen Young (CMNH); Jim Liebherr and Rick Hoebeke (CUIC); Tom Emmel and Andre Surakov (Florida State Collection of Arthropods) Julian Donahue (LACM); José Clavijo, Vilma Savini, and Luis Joly (MIZA); Allen Young (Milwaukee Public Museum); Robert Poole (NMNH); Wolfram Mey (ZMH). This research was supported by National Science Foundation grant BSR-9106517 to JSM.

LITERATURE CITED

- BEEBE, W., J. CRANE & H. FLEMMING. 1960. A comparison of eggs, larvae and pupae in fourteen species of heliconiine butterflies from Trinidad, W.I. *Zoologica N. Y.* 45: 111-154.
- BENSON, W. W. 1978. Resource partitioning in passion vine butterflies. *Evolution* 32: 493-518.

- BENSON, W. W., K. S. BROWN & L. E. GILBERT. 1976. Coevolution of plants and herbivores: Passion flower butterflies. *Evolution* 29:659-680.
- BIEZANKO, C. M. 1962a. Notodontidae et Diopitidae da Zona Sueste do Rio Grande do Sul. *Arq. Entomol. (Pelotas) Ser. A*, 8:1-14.
- 1962b. Notodontidae et Diopitidae da Zona Missioneira do Rio Grande do Sul. *Arq. Entomol. (Pelotas) Ser. B*, 8:1-8.
- BÖRNER, C. 1939. Die grundlagen meines lepidopterensystems, pp. 1372-1424. *In Verhandlungen der VII. Internationaler Kongress für Entomologie* 2. G. Uschmann, Berlin.
- BROWN, K. S. 1981. The biology of *Heliconius* and related genera. *Ann. Rev. Entomol.* 26:427-456.
- BRYK, F. 1930. Diopitidae. *In Strand, E. (ed.), Lepidopterorum Catalogus* (42). W. Junk, Berlin.
- CASTANEDA, R. R. 1956. Plantas de valor comercial del genero *Passiflora*: Granadilla, curcuba, badea y otras. *Agric. Trop.* 12:403-407.
- D'ALMEIDA, R. F. 1932. Les premiers états d'un Diopitidae. *Lambillionea* 32:14-16.
- DEVRIES, P. J. 1987. The butterflies of Costa Rica and their natural history. Papilionidae, Pieridae, Nymphalidae. Princeton Univ. Press, Princeton. 327 pp.
- DOCKTER, D. E. 1993. Developmental changes and wear of larval mandibles in *Heterocampa guttivitta* and *H. subrotata* (Notodontidae). *J. Lepid. Soc.* 47:32-48.
- DOGNIN, P. 1891. Diagnoses de quelques Hétérocères du Vénézuéla. *Le Natural.* 13: 109-110.
- EWEL, J., A. MADRIZ & J. A. TOSSI JR. 1976. Zonas de vida de Venezuela. Memoria explicative sobre el mapa ecológico. República de Venezuela, Ministerio de Agricultura y Cria, Fondo Nacional de Investigaciones Agropecuarias. Caracas, Editorial Sucre. 270 pp.
- FLEMING, H. E. 1960. The first instar larvae of the Heliconiinae (butterflies) of Trinidad, W.I. *Zoologica N. Y.* 45:91-110.
- FORBES, W. T. M. 1931. Notes on the Diopitidae (Lepidoptera). *J. New York Entomol. Soc.* 39:69-76.
- 1939. Family Diopitidae, pp. 318-322. *The Lepidoptera of Barro Colorado Island, Panama.* *Bull. Mus. Comp. Zool.* 85:99-322.
- FRACKER, S. B. 1915. The classification of lepidopterous larvae. *Illinois Biol. Monogr.* 2:1-161.
- GENTRY, A. H. 1993. A field guide to the families and genera of woody plants of northwest South America (Colombia, Ecuador, Peru) with supplementary notes on herbaceous taxa. Conservation International, Washington, D.C. 895 pp.
- GODFREY, G. L., J. S. MILLER & D. J. CARTER. 1989. Two mouthpart modifications in larval Notodontidae (Lepidoptera): their distributions and putative functions. *J. New York Entomol. Soc.* 97:455-470.
- HERBERT, F. B. 1920. Observations upon the instars of *Phryganidia* caterpillars. *Proc. Entomol. Soc. Washington* 22:193-200.
- HERING, E. M. 1925. Diopitidae, pp. 501-534. *In Seitz, A. (ed.), Macrolepidoptera of the world*, vol. 6. Alfred Kernen, Stuttgart.
- HEYWOOD, V. H. 1979. Flowering plants of the world. Oxford Univ. Press, London. 335 pp.
- HINTON, H. E. 1946. On the homology and nomenclature of the setae of lepidopterous larvae, with some notes on the phylogeny of the Lepidoptera. *Trans. R. Entomol. Soc. London* 97:1-37.
- HOLM-NIELSEN, L. B., P. M. JORGENSEN & J. E. LAWESSON. 1988. 126. Family Passifloraceae. *In Harling, G. & L. Andersson (eds.), Flora of Ecuador*, part 31. 130 pp.
- KILLIP, E. P. 1938. The American species of Passifloraceae. *Publ. Field Mus. Nat. Hist. (Bot.)* 19:1-613.
- KIRIAKOFF, S. G. 1950. Recherches sur les organes tympanique des Lépidoptères en rapport avec la classification. III. Diopitidae. *Bull. Ann. Soc. Entomol. Belgique* 86: 67-86.

- KITCHING, I. J. 1984. The use of larval chaetotaxy in butterfly systematics, with special reference to the Danaini (Lepidoptera: Nymphalidae). *Syst. Entomol.* 9:49-61.
- KÖHLER, P. 1930. Los Diopitidae argentinos. *Rev. Soc. Entomol. Argentina* 14:153-162.
- MARKIN, G. P., R. F. NAGATA & G. TANIGUCHI. 1989. Biology and behavior of the South American moth, *Cyanotricha necyria* (Felder and Rogenhofer) (Lepidoptera: Notodontidae), a potential biocontrol agent in Hawaii of the forest weed, *Passiflora mollissima* (HBK) Bailey. *Proc. Hawaiian Entomol. Soc.* 29:115-123.
- MARTIN, R. W. & H. Y. NAKASONE. 1970. The edible species of *Passiflora*. *Econom. Bot.* 24:333-343.
- MERZHEEVSKAYA, O. I. 1988. Larvae of owlet moths (Noctuidae): Biology, morphology, and classification. Amerind, New Delhi. [Transl. by P. M. Rao.]
- MILLER, J. S. 1988. External genitalic morphology and copulatory mechanism of *Cyanotricha necyria* (Felder) (Noctuoidea: Diopitidae). *J. Lepid. Soc.* 42:103-115.
- 1991. Cladistics and classification of the Notodontidae (Lepidoptera: Noctuoidea) based on larval and adult morphology. *Bull. Am. Mus. Nat. Hist.* 204:1-230.
- 1992a. Host-plant associations among prominent moths. *BioScience* 42:50-57.
- 1992b. Pupal morphology and the subfamily classification of the Notodontidae (Lepidoptera: Noctuoidea). *J. New York Entomol. Soc.* 100:228-256.
- MINET, J. 1983. Eléments sur la systematique des Notodontidae et nouvelles données concernant leur étude faunistique à Madagascar (Lepidoptera: Noctuoidea). *Bull. Soc. Entomol. France* 87:354-370.
- MOSHER, E. 1916. A classification of the Lepidoptera based on characters of the pupa. *Bull. Illinois St. Lab. Nat. Hist.* 12:14-159.
- PACKARD, A. S. 1895. Monograph of the bombycine moths of America north of Mexico including their transformations and origin of the larval markings and armature, part I: Family 1, Notodontidae. *Mem. Nat. Acad. Sci.* 7:1-390.
- PETERSON, A. 1962. Larvae of insects. An introduction to Nearctic species. Part I. Lepidoptera and plant infesting Hymenoptera. Printed for the author by Edwards Bros., Ann Arbor, Mich. 315 pp.
- PROUT, L. B. 1918. A provisional arrangement of the Diopitidae. *Novit. Zool.* 25:395-429.
- RAWLINS, J. E. 1992. Life history and systematics of the West Andean moth *Aucula franclemonti* with description of a new species from Ecuador (Lepidoptera: Noctuidae: Agaristinae). *J. New York Entomol. Soc.* 100:286-310.
- RICHARDS, A. G. 1932. Comparative skeletal morphology of the noctuid tympanum. *Entomol. Am.* 13:1-43.
- SCOBLE, M. J. 1992. The Lepidoptera: Form, Function and Diversity. Oxford Univ. Press, New York. 404 pp.
- SEITZ, A. 1925. Diopitidae, general topics, pp. 499-500. *In* Seitz, A. (ed.), *Macrolepidoptera of the world*, vol. 6. Alfred Kernen, Stuttgart.
- SICK, H. 1940. Beitrag zur kenntnis der Diopitidae, Notodontidae und Thaumetopoeidae und deren verwandtschaftsbeziehungen zueinander. *Zool. Jahrb. (Anat.)* 66:263-290.
- SILVA, A. G., C. R. GONÇALVES, D. M. GALVO, A. J. GONÇALVES, J. GOMES, M. N. SILVA & L. SIMONI. 1968. Quarto catálogo dos insectos que vivem nas plantas do Brasil. Rio de Janeiro.
- SPITZ, R. 1931. Especies novas de macrolepidopteros brasileiros e suas biologias. (1.ª parte). *Rev. Mus. Paul.* 17:459-482.
- STEHR, F. W. 1987. Order Lepidoptera, pp. 288-305. *In* Stehr, F. W. (ed.), *Immature insects*. Kendall/Hunt, Dubuque, Iowa.
- SURLYKKE, A. 1984. Hearing in notodontid moths: a tympanic organ with a single auditory neurone. *J. Exp. Biol.* 113:323-335.
- TALBOT, G. 1929. A new genus of Pericopinae (family Arctiidae). *Bull. Hill Mus.* 3:133.
- VANDERPLANK, J. 1991. *Passion Flowers and Passion Fruit*. MIT Press, Cambridge, Mass. 176 pp.
- WALKER, F. 1854. List of the specimens of lepidopterous insects in the collection of the British Museum. Part 2:279-581. Edward Newman, London.

- WARREN, W. 1900. New genera and species of American Drepanidae, Thyrididae, Epiplemidae and Geometridae. *Novit. Zool.* 7:117-225.
- 1905a. New Thyrididae, Uraniidae, and Geometridae from South and Central America. *Novit. Zool.* 12:41-72.
- 1905b. New American Thyrididae, Uraniidae, and Geometridae. *Novit. Zool.* 12:307-379.
- WATSON, A., D. S. FLETCHER & I. W. B. NYE. 1980. Noctuoidea (part). In Nye, I. W. B. (ed.), *The generic names of moths of the world*, vol. 2. *Brit. Mus. (Nat. Hist.)*, London.
- WELLER, S. J. 1989. Phylogeny of the Nystaleini (Lepidoptera: Noctuoidea: Notodontidae). Ph.D. dissertation, Univ. Texas, Austin.
- WOLDA, H. & R. FOSTER. 1978. *Zunacetha annulata* (Lepidoptera: Diopitidae), an outbreak insect in a Neotropical forest. *Geo-Eco-Trop.* 2:443-454.

Received for publication 20 October 1993; revised and accepted 18 June 1994.